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The Systematics and Evolution of the Subsaharan Africa, Seychelles, and Mauritius Scincine Scincid Lizards

ALLEN E. GREER

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THE SYSTEMATICS AND EVOLUTION OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCININE SCINID LIZARDS

ALLEN E. GREER

ABSTRACT

Skull osteology and external morphology form the basis for a review of the relationships of the scincine scincid lizards of subsaharan Africa, the Seychelles and Mauritius. There appear to be three natural groups in this area. *Proscelotes* and *Sepsina* constitute the most primitive group in subsaharan Africa, while *Scelotes*, *Melanoseps*, *Scolecoseps* and *Typhlacontias* form a second, perhaps more advanced group. The scincines of the Seychelles comprise two taxa worthy of generic rank (*Pamelaescincus* and *Janetaescincus*, new genera) and together with the monotypic Mauritius genus *Gongylomorphus* form a third natural group. Evolutionary and zoogeographic relationships within each of the three groups are discussed in some detail, but only a passing attempt is made to relate them with each other or with the large, but virtually unknown complex of scincines on Madagascar. In general, this complex seems to have more in common with the mainland *Proscelotes* and *Sepsina* and the three genera of the Seychelles and Mauritius than with the mainland *Scelotes* and its relatives. In addition to the systematic, evolutionary, and zoogeographic discussions there is also a key to the genera of scincines inhabiting mainland Africa south of the Sahara.

INTRODUCTION

Evidence has been presented elsewhere (Greer, 1970) demonstrating that at the subfamily level the Scincines are immediately ancestral to the other three subfamilies of skinks. With the exception of the largest genus (*Eumeces*, 46 species) in the subfamily and the monotypic *Neoseps* of Florida, the Scincinae are entirely Old World in distribution and, again with the exception of the widespread *Eumeces*, show a relict distribution in southcentral and eastern Asia (Fig. 1). For example, the only scincine, with the exception of *Eumeces*, in eastern Asia is *Brachymeles* (13 species) in the Philippines. As one moves west through Asia, no other scincines are encountered until one reaches India, where the monotypic *Barkudia* is known from the regions around Chilka Lake and Calcutta. Further south in India there is a single species of *Sepsophis* in the central and southern part of the subcontinent and two genera, *Nessia* (8 species) and *Chalcidoseps* (1 species), on Ceylon.

Moving still further west, it is not until one reaches Southwest Asia and the Mediterranean area that one encounters widely distributed genera with many species: e.g., *Ophiomorus* (9 species); *Scincus* (12 species); and *Chalcides* (14 species). And it is only south of the Sahara Desert in Africa, Madagascar, and the islands of the western Indian Ocean that the scincines become an important part of the skink fauna (76 of the 136 species of non-*Eumeces* scincines occur in this area).

Two of the other three subfamilies are also found in subsaharan Africa. The Acontinae with approximately 15 species and the

Figure 1. Distribution of the Scincinoe, exclusive of *Eumeces*.

Feylininae with 4 species are undoubtedly derived from scincines in Africa, which indicates, along with the present number of species and their distribution in subsaharan Africa, Madagascar, and the islands of the western Indian Ocean, that the scincines have been in subsaharan Africa for much, if not most, of their evolutionary history.

The reasons for the relict distribution of the scincines in south and east Asia and their prevalence in Southwest Asia, Africa, and Madagascar are undoubtedly complex, but may be due in part to the evolution and radiation of the Lygosominae in Southeast Asia and the Australian Region. The lygosomines are undoubtedly derived from the

scincines (Greer, 1970), and are morphologically the most advanced skinks. This group is most numerous and diverse in Southeast Asia and the Australian Region, and its expansion from this area of origin may account in part for the relict distribution of the scincines in south and east Asia. In Southwest Asia, Africa, and Madagascar, the area of the Old World furthest from their area of origin, the lygosomines are fairly well represented by species, but they are not morphologically diverse, i.e., there are not many genera. Presumably the lygosomines are only recent arrivals in this area, and have not yet swamped their ancestral scincine relatives. Perhaps if we could return in several million years, the scincines would show a relict distribution in Africa, Madagascar, and the west Indian Ocean islands as they do in southern and eastern Asia today.

Among scincines, relationships have remained most obscure in that area where extinction (due to competition from the lygosomines?) has done less to sharpen the differences between taxa, i.e., subsaharan Africa, Madagascar, and the islands of the western Indian Ocean.[1] The purpose of this paper is to delimit some of the scincine taxa in this area more clearly than has been the case in the past and to discuss their relationships. As much of the data from this study are derived from comparative skull osteology, the Malagasy scincines, most of which are as yet too poorly known in collections to allow a skull to be prepared, will be largely excluded from the formal taxonomic section of the paper, and their relationships with other scincines will be discussed only in a general way. This is unfortunate, as Madagascar, with its possibilities as a refuge for groups facing extinction from new competitors on the mainland, undoubtedly holds many answers to important questions of scincine evolution. It is doubly unfortunate that Madagascar should be the repository of this information, as it is unlikely to be much more accessible to collectors in the near future than it has been in the past. Madagascar, then, will probably be the "black box" of our analysis of scincine evolution for a long time to come.

The paper is divided into two major parts. In the first part taxonomic groups are defined, discussed, and defended, and in the second part the evolution and zoogeography of these groups are discussed. The reason for this format is simply that the evolution of groups cannot be discussed without knowing what the groups are that are evolutionarily significant. In addition to this, I have provided a key to the scincine genera of subsaharan Africa.

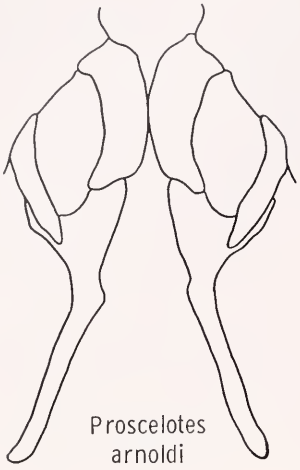
SYSTEMATICS OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCINCINAE

Since the appearance of Boulenger's (1887) third volume of the Catalogue of the Lizards in the British Museum, several authors have discussed the relationships of the scincines of subsaharan Africa, Madagascar, and the islands of the western Indian Ocean (Hewitt, 1921, 1927, and 1929; Barbour and Loveridge, 1928; Smith, 1935; de Witte and Laurent, 1943; Loveridge, 1957). All have relied heavily or exclusively on external characters and one internal character, namely, whether or not the palatine and pterygoid bones meet along the midline of the secondary palate.[2] Thus each successive discussant has had essentially the same characters available to him that were available to his predecessors. The present study adds new data from the comparison of whole skulls of most of the African, Seychelles, and Mauritius species[3] (see Specimens Examined section of paper).

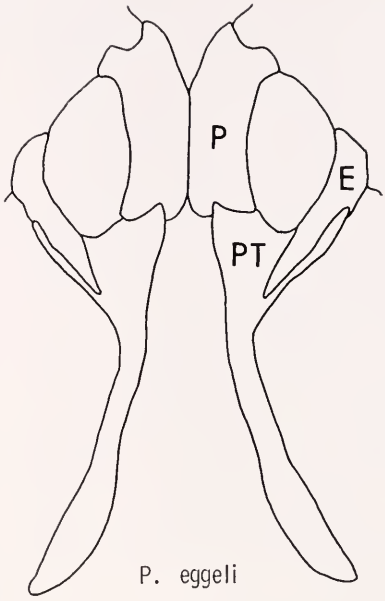
[1] The other side of this coin, however, is the preservation of intermediate forms, which makes it easier to understand the evolutionary relationships.

[2] Unfortunately, the relationships of the palatine and pterygoid bones have often been evaluated without removing the overlying buccal mucosa. This has led to misinterpretations.

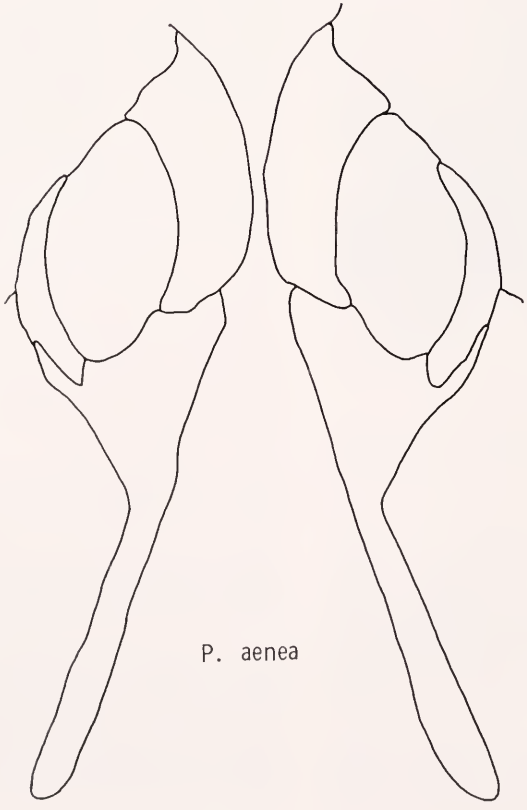
[3] Species of which whole skulls have been examined are marked with an asterisk (*) in the account of the genera.



Proscelotes
arnoldi



P. eggeli



P. aenea

The relevant work of previous authors is discussed under the appropriate taxonomic grouping.

GENERA OF SUBSAHARAN AFRICA

Proscelotes de Witte and Laurent

Proscelotes de Witte and Laurent, 1943, Mém. Mus. Roy. d'Hist. Nat., 2me sér., fasc. 26, p. 13 (Type species, *Scelotes eggeli* Tornier, 1902, by original designation).

Diagnosis. Skull characters: Palatine bones closely apposed or meeting along midline; palatal rami of pterygoids separated and diverging posteriorly; pterygoid teeth absent (Fig. 2). Postorbital bone present and relatively well developed; supratemporal arch strong and fenestra well developed; 17 to 22 maxillary teeth.

External characters: Interparietal small (except in *eggeli*), not touching supraocular scales; a pair of supranasals meeting behind rostral; external ear opening present; 5 fingers and toes (i.e., digital formula, 5–5).

Distribution. Lowlands of Mozambique (*aenea*); from Inyanga south to Melsetter in Rhodesia and Mlanje Mt. in Malawi (*arnoldi*) and Usambara Mts., Tanzania (*eggeli*).

*Species. Aenea** Barbour and Loveridge, 1928; *arnoldi** Hewitt, 1932; *eggeli** Tornier, 1902.

Mode of reproduction. Both *arnoldi* and *eggeli* are known to be live bearing, *arnoldi* producing 5 young (1 female observed—FitzSimons, 1943: 205) and *eggeli*, 3–4 young (3 females observed—Barbour and Loveridge, 1928: 166; and Greer, personal observation). There is no information available on reproduction in *aenea*.

Discussion. With the exception of *eggeli* and *ulugurnensis*, de Witte and Laurent (1943) divided all the subsaharan mainland African scincines, and the genera of what are now considered two other subfamilies, into two "phyla." One "phylum" was characterized by an interparietal narrower than the frontal and included the genera (as they conceived them) *Sepsina*, *Dumerilia*, *Acontias*, *Acontophiops*, and *Typhlosaurus*. The last three of these five genera are, however, now placed in the subfamily Acontinae (Greer, 1970), and need not concern us here.

The other "phylum" of de Witte and Laurent was characterized by the interparietal's being wider than the frontal. This group included the genera *Herpetosaura*, *Scelotes*, *Scolecoseps*, *Fitzsimonsia*, *Typhlacontias*, *Feylinia*, and *Chabanaudia*. The last two genera are now considered members of the subfamily Feylininae (Greer, 1970).

Two mainland African scincines, *eggeli* and *ulugurnensis*, however, have frontals that are constricted anteriorly by the supraocculars as in certain Madagascar scincines but not as in any other mainland subsaharan African scincines. This character, along with the fact that the two species are primitive in retaining 5 fingers and toes and seem to have interparietals intermediate in size between the sizes of the interparietal of the two "phyla," suggested to these authors that *eggeli* and *ulugurnensis* formed a relict group ancestral to the two mainland "phyla." The status of these two species was emphasized by their being placed in a new genus of their own—*Proscelotes*.

The interparietal scale is indeed an important taxonomic character in the Scincinae. Unfortunately, however, de Witte and Laurent chose a poor description of the character in the relative size of the scale. A characteristic of the interparietal that is more important, and is reflected less clearly in the size of the scale, is the position of the interparietal relative to the supraoculars;

←

Figure 2. Ventral view of the secondary palate in the three species of the genus *Proscelotes*. Upper left: *P. arnoldi* MCZ 55145; upper right: *P. eggeli* MCZ 24217; bottom: *P. aenea* MCZ 18709. Abbreviations for this and other figures: *p*, palatine; *e*, ectopterygoid; *pt*, pterygoid. Not drawn to scale.

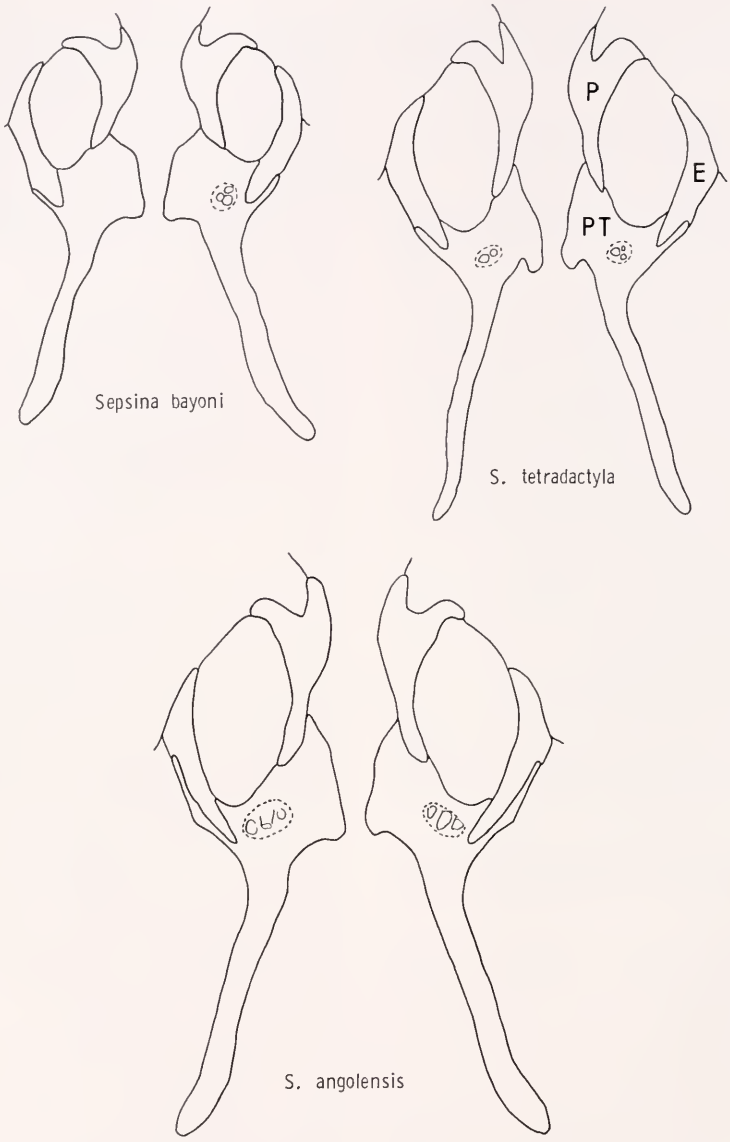


Figure 3. Ventral view of the secondary palate in three species of Sepsina. Upper left: S. *bayani* BM 1967.80; upper right: S. *tetradactyla* MCZ 42885; bottom: S. *angolensis* FMNH 142793. Abbreviations as in Fig. 2. Drawn to scale.

that is, whether the interparietal is in contact with the supraoculars (wider than the frontal) or not in contact with the supraoculars (narrower than the frontal). This character state does not cut across groupings based on skull characters (see diagnoses) and serves to divide the scincines of subsaharan Africa along essentially the same lines as those proposed by de Witte and Laurent (1943).

With this interpretation of the interparietal, de Witte and Laurent's two species of *Proscelotes* can be easily assigned to one of the two "phyla," and on skull characters

can be shown to be members of species groups within these "phyla." Thus *eggeli*, with a large interparietal, but one not touching the supraoculars, belongs to one "phylum," whereas *ulugurnensis*, with the interparietal touching the supraoculars, belongs to the other "phylum."

Within the "phylum" characterized by the interparietal's not touching the supraoculars, *eggeli* is, on the basis of its skull morphology, similar to two other species (*aenea* and *arnoldi*) and forms with these a natural group. The diagnostic characters of this taxon warrant generic recognition. The available name is *Proscelotes,* of which *eggeli* is the type species.

In showing a distinct postorbital bone, i.e., unfused to the postfrontal, and a well-developed supratemporal arch, *Proscelotes* does seem to be rather primitive, as suggested by de Witte and Laurent (1943). The retention of 5 fingers and toes in the three species also supports this supposition.

Sepsina Bocage

Sepsina Bocage, 1866, J. Acad. Sci. Lisboa, vol. 1, p. 62 (Type species, *Sepsina angolensis* Bocage, 1866, by monotypy).

Dumerilia Bocage, 1866, J. Acad. Sci. Lisboa, vol. 1, p. 63 (Type species, *Dumerilia bayonii* Bocage, 1866, by monotypy).

Sepsina (*Rhinoscincus*) W. Peters, 1874, Monatsber. Ak. Wiss. Berlin, p. 373 (Type species, *Sepsina* (*Rhinoscincus*) *tetradactyla* W. Peters, 1874, by monotypy).

Scincodipus W. Peters, 1875, Monatsber. Ak. Wiss. Berlin, p. 551 (Type species, *Scincodipus congicus* W. Peters, 1875 = *Sepsina bayonii* Bocage, 1866, by monotypy).

Diagnosis. Skull characters: Palatine bones widely separated along the midline; palatal rami of pterygoids expanded medially with a tendency toward emargination posteriorly; pterygoid teeth present (Fig. 3). Postorbital bone present and relatively well developed; supratemporal arch strong and fenestra well developed; 12 to 18 maxillary teeth.

External characters: Interparietal small, not touching supraocular scales; a pair of supranasals meeting behind rostral; external ear opening present; digits 4–4 or fewer.

Distribution. Northern Southwest Africa northward through Angola (*angolensis*) and Cabinda (*bayoni* only) into the southeast part of the Democratic Republic of the Congo (*angolensis*) through the southeastern and eastern sections of the Democratic Republic of the Congo to eastern Tanzania and Malawi (*tetradactyla*).

From comparison of the distribution of *Sepsina* with the distribution of the main vegetation types of Africa (Moreau, 1966: 17, fig. 3), it is clear that *Sepsina* is confined primarily to woodlands (moist and dry), savanna, and steppe, but is excluded from the lowland evergreen forest of west equatorial Africa.

*Species. Angolensis** Bocage, 1866; *bayoni** Bocage, 1866; *tetradactyla** Peters, 1874.

Incertae sedis. Alberti Hewitt, 1929; *copei* Bocage, 1873.

On external characters *Proscelotes* can be distinguished from *Sepsina* only on the basis of 5 fingers and toes in the former and no more than 4 fingers and toes in the latter. Digital formulas, however, are so notoriously variable in scincid genera that I hesitate to use such a character in assigning species like *alberti* and *copei*, for which no skull has been available, to genera that are diagnosed primarily on skull characters. For the moment, however, the digital formula is our only clue to the relationships of *alberti* and *copei*, and with only 4 fingers and toes, these two species are considered as most likely belonging in *Sepsina*.

Mode of reproduction. Nothing is known about the mode of reproduction in *Sepsina*.

Discussion. De Witte and Laurent (1943) resurrected the generic name *Dumerilia* Bocage, 1866 for *bayoni* on the grounds that the frontal in this species is wider than it is long, unlike the other species of scincines of the "phylum" consisting of those species with the interparietal narrower than the frontal (essentially the genera *Proscelotes* and *Sepsina* as construed here).

Table 1. Interspecific variation in several characters of the genus *Scelotes*. See text for discussion.

Species	Digital formula	Ear opening: present (+) or absent (—)	*Herpetosaura* (H) or *Scelotes* (S), fide de Witte and Laurent	Palatines meet (+) or not (—)	Postorbital present (+) or absent (—)	Supratemporal fenestra
capensis	5–5	+ minute	H			
mira	5–5	+ small	H	—	+ small	+ minute
uluguruensis	5–5	+ minute	H[1]	+	—	+ small
caffer	3–3	—	H	+	+ minute	—
limpopoensis	3–3	+ small	H	—	+ small	+ small
bidigittata	0–2	+ minute	H	—	—	+ minute
bipes	0–2	+ minute	S		—	+ minute
kasneri	0–2	+ small	S			
brevipes	0–1	+ minute	H	+	+ small	+ minute
gronovi	0–1	+ minute	S	+	+ thin	—
guentheri	0–1	—	H			
anguina	0–0	—	H	—	+ minute	—
arenicolor	0–0	—	S	—	—	+ minute
bicolor	0–0	—	S			
inornatus	0–0	+ minute	H			

[1] Placed in *Proscelotes* by de Witte and Laurent (1943), but on the criterion of "frontal longer than wide" for distinguishing *Herpetosaura* from *Scelotes* the species is similar to the former genus.

This action seems undesirable since the broad frontal of *bayoni* is probably an adaptation to burrowing habits, which, on the basis of other features of the external anatomy (snout more wedge-shaped and digits reduced to the greatest extent: no forelimbs and a single styliform hindlimb[1]), seem to be more well developed in *bayoni* than in the other species of scincines with the small interparietal south of the Sahara. In the genus *Scelotes* there is a similar trend toward the development of a relatively wider frontal in those species that, on the basis of other morphological characters, seem to be more highly adapted to a burrowing life (see page 10 and Table 1).

Although the two taxa of scincines with the small interparietal (which fails to touch the frontal) south of the Sahara Desert in mainland Africa, i.e., *Proscelotes* and *Sepsina*, can be recognized on the basis of external characters (*Proscelotes* with 5 fingers and toes and *Sepsina* with 4 fingers and toes or fewer), it should be emphasized that the more important characters distinguishing the two genera are in the skull.

The discrete, well-developed postorbital bone and the pterygoid teeth of *Sepsina* are definitely primitive characters. *Sepsina*, in fact, is the only mainland genus of scincines south of the Sahara to retain pterygoid teeth.

[1] Although de Witte and Laurent (1943) describe the monotypic genus *Dumerilia* as "pas de membres postérieurs," the two specimens I have seen (BM RR 1967.80 and MCZ 27098) have styliform hindlimbs and even Boeage (1866) in his description of the species states, "membres postérieurs médiocres, en forme de stylets simples, déprimés."

Scelotes Fitzinger

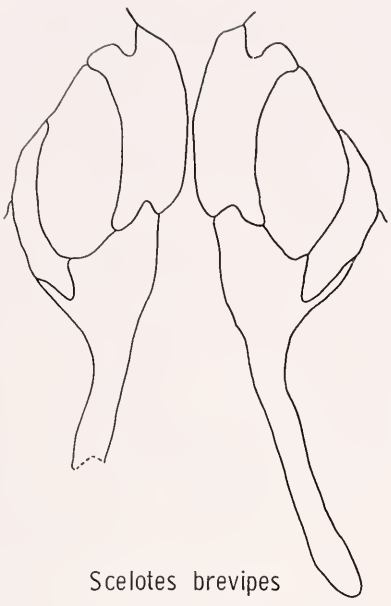
Scelotes Fitzinger, 1826, Neue Class. Rept., pp. 23, 53 (Type species, *Bipes anguineus* Merrem, 1820 = *Scelotes bipes* Linnaeus, 1766, by monotypy).

Zygnis (not Oken, 1816 or Fitzinger, 1826) Wagler, 1830, Nat. Syst. Amphib., p. 160 (Type species, *Anguis bipes* Linnaeus, 1766, by monotypy).

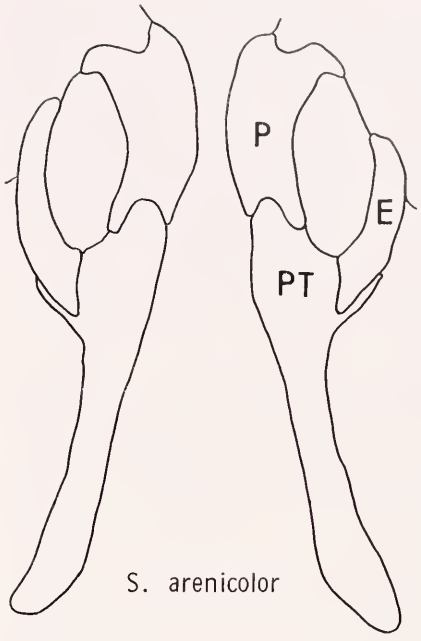
? *Herinia* Gray, 1838, Ann. Mag. Nat. Hist., vol. 2, p. 332 (Type species, *H. capensis* Gray, 1838 = ?, by monotypy).

→

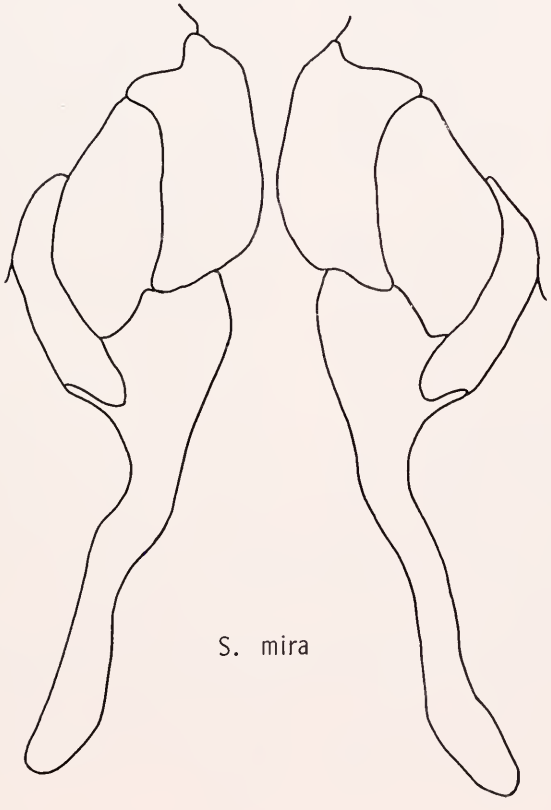
Figure 4. Ventral view of the secondary palate in three species of *Scelotes*. Upper left: *S. brevipes* MCZ 21237; upper right: *S. arenicolor* MCZ 14205; bottom: *S. mira* MCZ untagged specimen. Abbreviations as in Fig. 2. Drawn to scale.



Scelotes brevipes



S. arenicolor



S. mira

Lithophilus (not Fröhlich, 1799) A. Smith, 1849, Illus. Zool. S. Africa, Rept., App., p. 12 (Type species *Lithophilus inornatus* A. Smith, 1849, by subsequent designation of de Witte and Laurent, 1943).

Herpetosaura W. Peters, 1854, Monatsber. Ak. Wiss. Berlin, p. 619 (Type species, *Herpetosaura arenicolor* Peters, 1854, by monotypy).

Sepomorphus W. Peters, 1861, Monatsber. Ak. Wiss. Berlin, p. 422 (Type species, *Sepomorphus caffer* Peters, 1861, by monotypy).

Herpetoseps Boulenger, 1887, Cat. Lizards Brit. Mus., vol. 3, p. 416 (Type species, *Herpetoseps anguinus* Boulenger, 1887, by monotypy).

Diagnosis. Skull characters: Palatine bones meeting or closely apposed on midline; palatal rami of pterygoids separated medially and diverging posteriorly; pterygoid teeth absent (Fig. 4). Postorbital bone present, but small to minute, or absent; supratemporal arch weak, fenestra obliterated by apposition of bones of arch with parietal bone; 11 to 23 maxillary teeth, but only *ulugurnensis* with 22 to 23 maxillary teeth, all other species with 11 to 19 teeth.

External characters: Interparietal large, touching supraocular scales; external ear opening present or absent; a pair of supranasals meeting behind rostral (fused only in some *bipes*); digital formula 5–5 to 0–0 (see Table 1).

Distribution. Africa south of an area from southern South-west Africa (*capensis*), east through extreme southern Rhodesia (*limpopoensis* from Beitbridge), and southern Mozambique. Most of the species are found in southern and eastern Africa.

*Species. Anguina** Boulenger, 1887; *arenicolor** W. Peters, 1854; *bidigittata** FitzSimons, 1930; *bicolor* A. Smith, 1849; *bipes** Linnaeus, 1766; *brevipes** Hewitt, 1925; *caffer** W. Peters, 1861; *capensis* A. Smith, 1849; *gronovi** Daudin, 1802; *guentheri* Boulenger, 1887; *inornata* A. Smith, 1849; *kasneri* FitzSimons, 1839; *limpopoensis** FitzSimons, 1930; *mira** Roux, 1907; *ulugurnensis** Barbour and Loveridge, 1928.

Mode of reproduction. The mode of reproduction is known for six of the fifteen species of *Scelotes* and all are live bearing (available clutch sizes follow the species name): *arenicolor*—4 (FitzSimons, 1943: 197); *bidigittatus*—1 to 2 (Pienaar and FitzSimons, 1966: 57); *bipes*—2 (FitzSimons, 1943: 191); *brevipes*—2 (FitzSimons, 1943: 195); *mira*—4 (FitzSimons, 1943: 183); *ulugurnensis*—? (Barbour and Loveridge, 1928: 167).

Discussion. Two characters that show a good deal of interspecific variation in *Scelotes* (as conceived here) have been emphasized in generic diagnoses. One of these characters, the complete absence of hindlimbs (used to distinguish the genera *Lithophilus*, *Herpetosaura*, and *Herpetoseps*), is most probably correlated with an increasing tendency toward a burrowing way of life, although actual ecological observations are lacking to support this. The reduction of limbs is also correlated with a reduction in the size of the external ear opening, presumably also an adaptation to burrowing habits (Table 1).

Whether or not the palatine bones touch along the midline of the palate has also been used as a generic character in this group, but it has long been known that this feature is an interspecifically variable character in *Scelotes* (Hewitt, 1921 and 1927; Barbour and Loveridge, 1928; Table 1, this paper).

De Witte and Laurent (1943) revived the name *Herpetosaura* for those species of *Scelotes* with the frontal longer than wide, leaving *Scelotes* to include those species with the frontal wider than long. In Table 1 the generic allocation of the species considered here to be *Scelotes* is given according to de Witte and Laurent. It can be seen from the Table that a frontal wider than long (the "*Scelotes*" condition) is, in general, correlated with other morphological features indicative of a burrowing way of life. In my opinion this use of characters that show evolutionary trends within a taxon to subdivide that taxon into formal taxonomic groupings, unnecessarily obscures the evolutionary significance of those characters for the sake of taxonomic convenience.

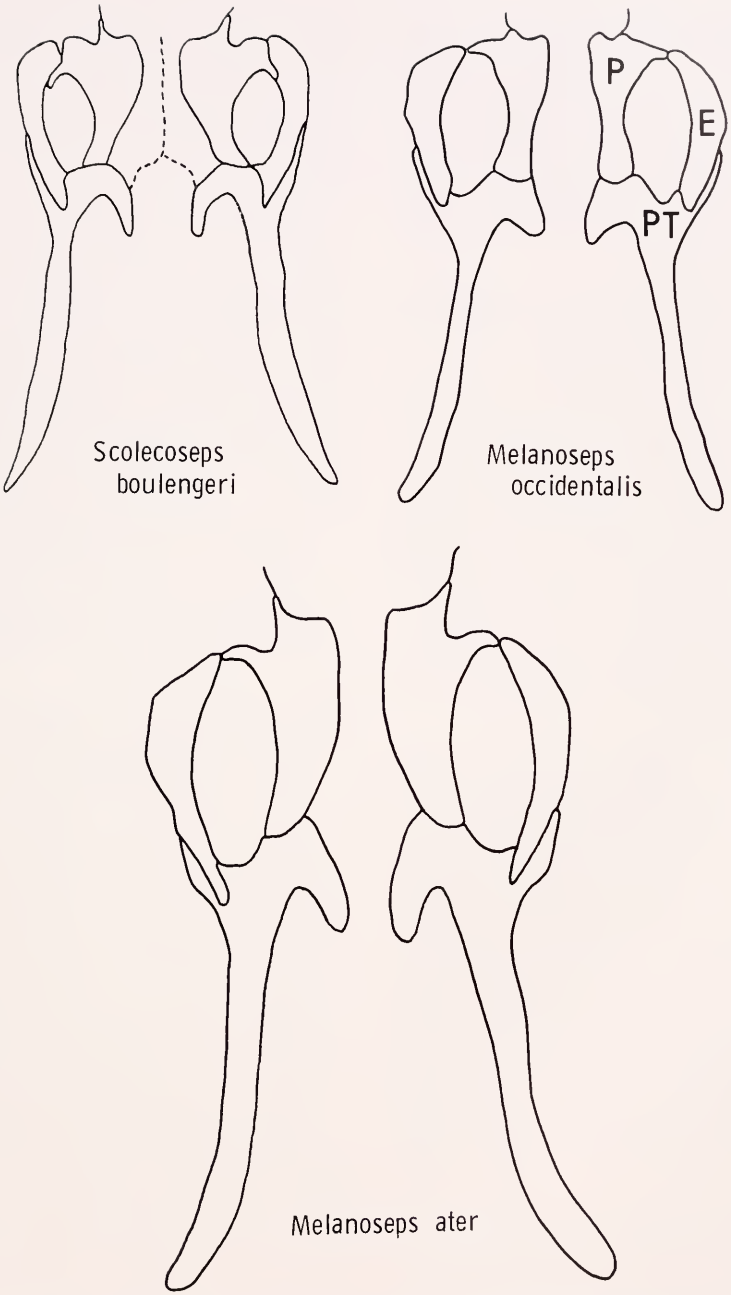


Figure 5. Ventral view of the secondary palate in *Scolecoseps* and *Melanoseps*. Upper left: *Scolecoseps boulengeri* MCZ 18357; upper right: *Melanoseps occidentalis* BM 1907.5.22.6A; bottom: *M. ater rondoensis* MCZ 52487. Drawn to scale. Abbreviations as in Fig. 2.

It should be noted here that *ulugurnensis*, a species with a large interparietal touching the supraoculars, was considered a species of *Proscelotes* by de Witte and Laurent (see pages 6–7 above). In the diagnostic skull characters, however, *ulugurnensis* is unlike the type species of *Proscelotes* (*eggeli*) and very much like the other species of *Scelotes*.

Melanoseps Boulenger

Melanoseps Boulenger, 1887, Cat. Lizards Brit. Mus., vol. 3, p. 422 (Type species *Herpetosaura atra* Günther, 1873, by monotypy).

Diagnosis. Skull characters: Palatine bones separated medially; palatal rami of pterygoids expanded medially and emarginated posteriorly; pterygoid teeth absent (Fig. 5). Postorbital bone absent; supratemporal arch weak and fenestra obliterated by apposition of bones of the arch with the parietal bone; 10 to 13 maxillary teeth.

External characters: Interparietal large, touching supraoculars; a pair of supranasals meeting behind rostral; no external ear opening; limbless.

Distribution. Extreme southern Kenya south through Tanzania and Malawi to the Zambesi (*ater*) and west through the Democratic Republic of the Congo, and extreme northeastern Angola to Cameroon and Fernando Poo (*occidentalis*). In addition, Sternfield (1911) reports a single specimen of *occidentalis* from Windhuk, Southwest Africa. This locality is, however, some distance from the range indicated by other specimens of *occidentalis* and is also from a considerably drier area than any other specimens. For these reasons the record should perhaps be regarded with suspicion (Mertens, 1955).

*Species. Ater** Günther, 1873 (six subspecies); *occidentalis** W. Peters, 1877.

Mode of reproduction. Personal observations on *M. ater misukuensis* indicate that the species is live bearing. Six gravid females had 2 to 4 (average = 3.0) developing eggs in a clutch.

Discussion. The generic distinction of *Melanoseps* from *Scelotes*, which has been argued for by most authors (Boulenger, 1887; Tornier, 1901; Loveridge, 1957; Laurent, 1964), is confirmed on the basis of skull morphology: no *Scelotes* has the medially expanded and posteriorly emarginated palatal rami of the pterygoids seen in *Melanoseps* (Figs. 4, 5).

De Witte and Laurent (1943) regarded *Melanoseps* as a synonym of *Scelotes*. However, when Loveridge (1957) pointed out that *Melanoseps* is "associated with primary forest, either montane or gallery," a habitat from which *Scelotes* is largely excluded, Laurent (1964) considered these ecological differences, along with the morphological differences, sufficient evidence for the generic separation of *Melanoseps* from *Scelotes*.

Melanoseps appears to be a derivative of a *Scelotes*-like ancestor that has evolved primarily in the evergreen montane and lowland forests of central Africa.

Scolecoseps Loveridge

Scolecoseps Loveridge, 1920, Proc. Zool. Soc. London, p. 159 (Type species, *Scolecoseps boulengeri* Loveridge, 1920, by monotypy).

Diagnosis. Skull characters: Palatines widely separated; palatal rami of pterygoids expanded slightly toward midline and deeply emarginated posteriorly, somewhat as in *Melanoseps*; pterygoid teeth absent (Fig. 5). Postorbital bone absent; supratemporal arch weak and fenestra obliterated by apposition of bones in arch with parietal bone; twelve maxillary teeth.

External characters: External naris in a large rostral and connected with the posterior edge of the rostral through a horizontal suture somewhat as in *Typhlacontias* (Scincinae) or the subfamily Acontinae. Interparietal large, touching supraoculars; a pair of supranasals meeting behind rostral; no external ear opening; limbless.

Distribution. Lumbo, Mozambique (*boulengeri*) and Dar es Salaam to Kilwa, Tanzania (*acontias*).

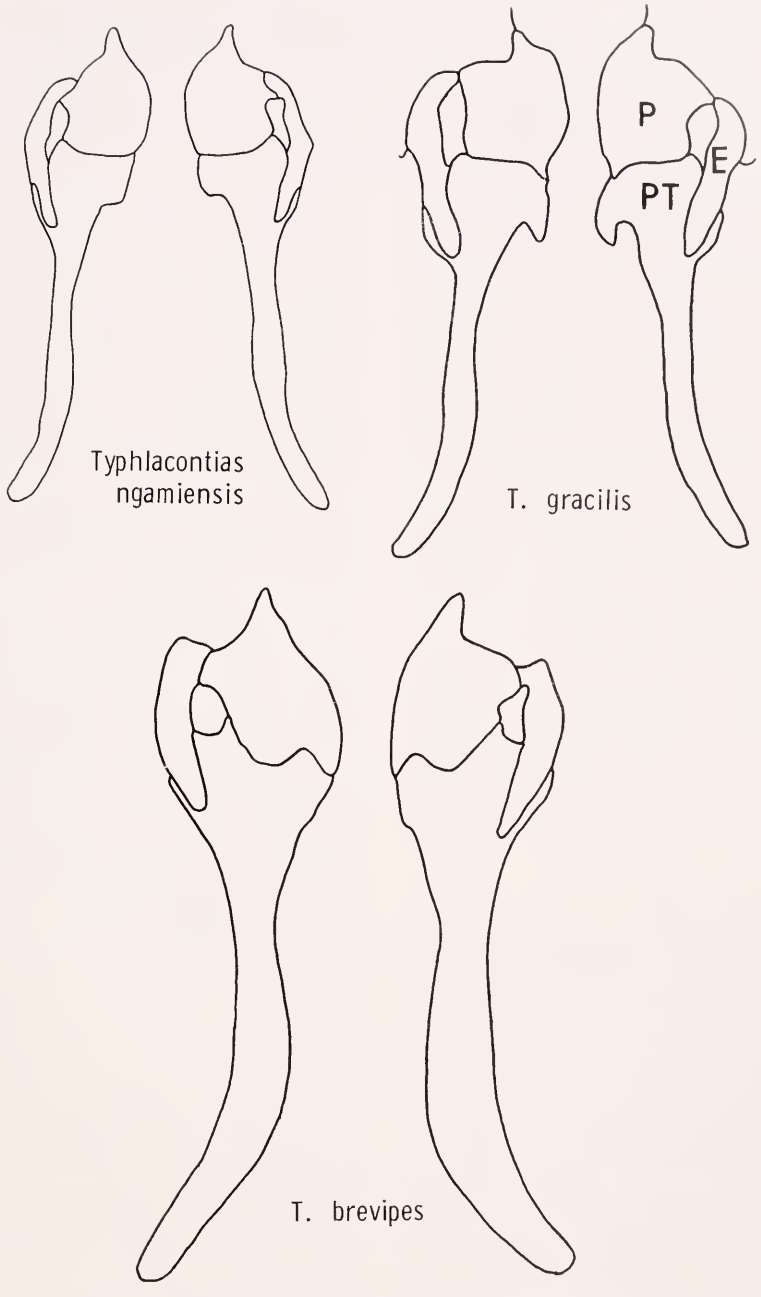


Figure 6. Ventrol view of the secondary palate in three species of *Typhlacontias*. Upper left: *T. ngamiensis* FMNH 142787; upper right: *T. gracilis* USNM 159338; bottom: *T. brevipes* MCZ 96702. Abbreviations as in Fig. 2. Drawn to scale.

Species. Acontias Werner, 1912; *boulengeri** Loveridge, 1920.

Mode of reproduction. Absolutely nothing is known about the mode of reproduction in the two species of this rare genus.

Discussion. I have been able to examine the secondary palate only in the type species of this genus, *boulengeri.* The palate is similar to that of *Melanoseps*, but the large rostral seems distinct enough to warrant generic separation from *Melanoseps.*

I have not been able to see the palate in *acontias*, the other species in the genus. The enlarged rostral of this species is similar to that of *Scolecoseps boulengeri*, but it is also similar to the rostral of some *Typhlacontias.* Since palatal characters are the only basis we would have for changing the generic status of *acontias*, it seems best to follow current taxonomic opinion (de Witte and Laurent, 1943; Loveridge, 1957) and retain *acontias* in *Scolecoseps.*

These two species of skinks are extremely poorly represented in herpetological collections, and virtually nothing is known of their ecology. The absence of both an external ear opening and limbs would indicate that the genus is burrowing or at least cryptic in habits.

Typhlacontias Bocage

Typhlacontias Bocage, 1873, J. Acad. Sci. Lisboa, vol. 15, p. 5 (Type species, *Typhlacontias punctatissimus* Bocage, 1873, by monotypy).

Fitzsimousia de Witte and Laurent, 1943, Mém. Mus. Roy. d'Hist. Nat., 2me sér., fasc. 26, p. 33 (Type species *Typhlacontias brevipes* FitzSimons, 1939, by monotypy).

Diagnosis. Skull characters: Palatine bones only slightly longer than wide, separated medially; palatal rami of pterygoids expanded laterally, but not meeting medially, and emarginated posteriorly (*gracilis*) or not (*brevipes* and *ngamiensis*); pterygoid teeth absent (Fig. 6). Postorbital and jugal bones lacking; supratemporal arch weak and fenestra obliterated by the apposition of the bones in the supratemporal arch with the parietal; five to six maxillary teeth.

External characters: Interparietal large, touching supraoculars; three median, transversely enlarged head scales between the rostral and interparietal instead of a pair of supranasals and two median, transversely enlarged head scales; no external ear opening; limbless except for *T. brevipes*, which has a rudimentary hind leg.

Distribution. Collecting records for the genus are few and widely separated but stretch from southern Angola and Southwest Africa east through Botswana to the Upper Zambesi region and extreme southeastern Rhodesia. This area is covered by the desert, subdesert, and dry woodlands, steppe vegetation types of Moreau (1966, fig. 3).

Species. Bogerti Laurent, 1966; *brevipes** FitzSimons, 1938; *gracilis** Roux, 1907; *ngamiensis** FitzSimons, 1932; *punctatissimus* Bocage, 1873; *rohani* Angel, 1923.

Mode of reproduction. The only information on the mode of reproduction in this genus is the statement by Laurent (1964: 84) in regard to *T. bogerti*, which would indicate that the species is live bearing: "Le grand Paratype contient des *embryons avancés* dont les yeux sont fort développés." The italics are mine.

Discussion. The large interparietal indicates that *Typhlacontias* is a relative of *Scelotes*, and like *Melanoseps* the genus is probably a *Scelotes* derivative. But unlike *Melanoseps*, which has evolved in the moist evergreen lowland and montane forest of central Africa, *Typhlacontias* seems to have evolved in the arid areas of southern Africa. The adaptations of the genus, e.g., absence of an external ear opening, the almost complete reduction (*brevipes*) or absence of the limbs, and the large rostral, seem to be indicative of highly developed burrowing habits, but ecological data by which to judge this supposition are lacking. That the group is not just a composite of independently evolved *Scelotes*, well adapted to a burrowing life, is indicated by the large single postrostral scale, the unique proportion and relationships of the palatal bones,

the absence of a jugal bone, and the low number of maxillary teeth—features not found in those *Scelotes* (*brevipes*, *gronovi*, *guentheri*, *anguina*, *arenicolor*, *bicolor*, and *inornatus*) similarly adapted in other features of their morphology to a burrowing life.

Typhlacontias brevipes has the external naris situated close to the posterior edge of the rostral and bordered posteriorly by a small postnasal scale; this is a *Scelotes*-like feature. It also retains minute posterior limbs unlike other *Typhlacontias*. Because of these features de Witte and Laurent (1943) created a new genus, *Fitzsimonsia*, for the species. Such special taxonomic recognition seems unjustifiable to me as it obscures evolutionary relationships. *Typhlacontias brevipes* is best viewed as the most primitive, i.e., the most *Scelotes*-like, of its genus and relates *Typhlacontias* directly with *Scelotes*. *T. brevipes* possesses the large single postrostral scale and palatal characters of *Typhlacontias* and lacks the jugal bone as do other *Typhlacontias*, but it resembles *Scelotes* in the position of the external naris and the minute hindlimbs.

It is interesting to note that among the scincines of subsaharan Africa only *Scelotes bipes* has postrostral scales (supranasals) that are sometimes fused to form a single median transverse scale. This condition is characteristic of *Typhlacontias* and is further evidence that a *Scelotes* was probably ancestral to *Typhlacontias*.

MAURITIUS AND SEYCHELLES GENERA

With the exception of Bermuda, which harbors the endemic *Eumeces longirostris*, Mauritius and the Seychelles are the most remote oceanic islands on which scincines are known to occur now or in the recent past. On the Seychelles there are three species (*gardinieri*, *braueri*, and *veseyfitzgeraldi*) that have always been called either *Scelotes* or *Amphiglossus*, generally by authors using these two generic names in their widest, catchall sense. The single scincine on Mauritius (*bojeri*) and the neighboring islands[1] on the bank just north of the main island has generally been placed in the genus *Scelotes* or referred to a monotypic genus, *Thyrus*. Loveridge (1957) has noted that the generic name *Thyrus* for the endemic Mauritius scincine is antedated by the name *Gongylomorphus*.

The scincines of the Seychelles and Mauritius show certain peculiar features in their skull osteology that have not been encountered in any other scincine species for which skulls are available. The most striking of these features is an extensive secondary palate (Fig. 7) formed by the medial apposition of the palatine bones (seen in a less well-developed state among scincines only in *Proscelotes* and some *Scelotes*) and the palatal rami of the pterygoids (unknown in any other scincine to date). In addition, there are 11 teeth on the premaxillae in the Mauritius and Seychelles scincines, whereas all other scincines have only 10 (only a few *Brachymeles*) or fewer (generally fewer than 9 in most other scincines).

Slightly less significant, but of value in recognizing groupings of scincines in Africa, is the presence of a large, distinct postorbital bone (partially fused to the postfrontal in the single skull of *braueri* examined) and a well-developed supratemporal arch.

These similarities, especially for scincines, would be indicative of close relationship in other species groups. But the fact that these species occur on two widely separated oceanic island banks poses a serious zoogeographic problem and raises the possibility of convergence as an alternative explanation for the unique similarities among the four species. There is, however, no other evidence suggesting that the similarities among these species are convergent. Indeed, the independent evolution of a remarkably advanced secondary palate (for scincines) in these lizards seems less cred-

[1] This species is actually known only from subfossil material on Mauritius itself (Hoffstetter, 1945 and 1949), although it still occurs on several small islands just north of Mauritius (Vinson, 1965).

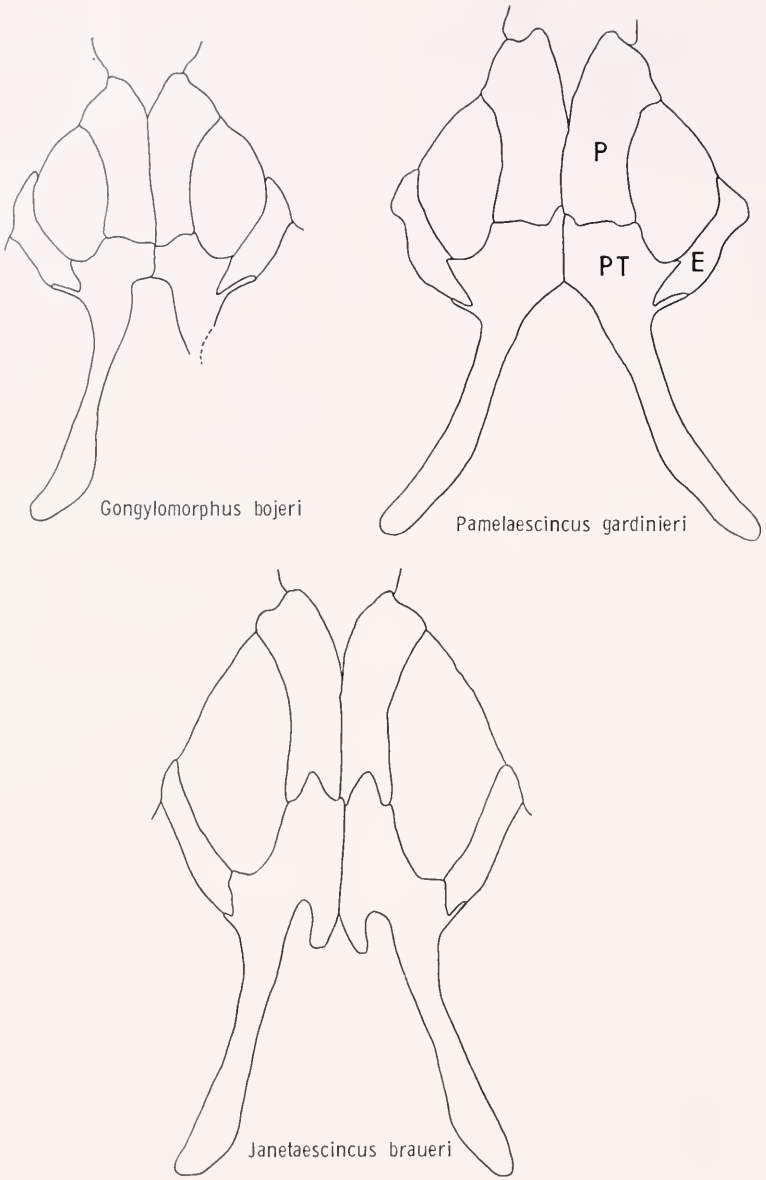


Figure 7. Ventral view of the secondary palate in *Gongylamorphus*, *Pamelaescincus* and *Janetaescincus*. Upper left: *Gongylamorphus bojeri* MCZ 46677; upper right: *Pamelaescincus gardinieri* BM 1910.3.18.91; bottom: *Janetaescincus braueri* BM 1910.3.18.33. Abbreviations as in Fig. 2. Not drawn to scale.

ible to me than the notion of their close relationship in spite of the zoogeographic problem raised by that relationship. For the present, therefore, I am regarding the scincines of Mauritius and the Seychelles as a closely related group with a remarkable distribution.

In spite of the remarkable similarities which serve to distinguish them as a group apart from all other scincines, the Seychelles

and Mauritius scincines (4 species) themselves show certain peculiar morphological features that warrant their separation into 3 genera as follows:

Gongylomorphus Fitzinger

Gongylomorphus Fitzinger, 1843, Syst. Rept., p. 22 (Type species, *Gongylus bojerii* Duméril and Bibron, 1839 = *Scincus bojerii* Desjardin, 1831, by monotypy).

Thyrus Gray, 1845, Cat. Specimens Lizards Coll. British Mus., p. 124 (Type species, *Scincus bojerii* Desjardin, 1831, by monotypy).

Diagnosis. Skull characters: Palatine bones and palatal rami of pterygoids meeting medially; palatal rami of pterygoids "squared-off," not emarginated posteriorly as in the following two genera; pterygoid teeth absent (Fig. 7). Postorbital bone distinct, well developed; supratemporal arch well developed; 16 teeth on maxilla and 11 teeth on premaxillae.

External characters: Interparietal small, not touching supraoculars; frontoparietals present (absent in all other subsaharan Africa, Madagascar, or west Indian Ocean island scincines); ear opening a horizontal slit; 38 longitudinal scale rows at midbody; digits 5–5.

Distribution. At present *G. bojeri* occurs only on several small islands (Round, Plate, Coin de Mire, and Forquets) lying on the shallow bank just north of Mauritius. The species is, however, known from subfossil remains on Mauritius (Mare aux Songes), and Vinson (1965) conjectures that in the past *G. bojeri* also occured on Reunion.

*Species. Bojeri** Desjardin, 1831.

Discussion. One of the most intriguing questions centering around *bojeri* is its recent extinction on the main island of Mauritius while it persists on the small bank islands just north of the main island. Interestingly enough, however, *bojeri* is not unique in being subfossil on Mauritius while persisting on a bank island. *Casarea*, a monotypic genus of boiid snakes, is also subfossil on Mauritius in the same locality as *bojeri* (Mare aux Songes), but persists on Round Island in the bank islands (Hoffstetter, 1960). Similarly the giant skink *Didosaurus mauritianus* is subfossil on Mauritius (Mare aux Songes) while its very close relative (Greer, personal observation), *Leiolopisma telfairi*, exists only on Round Island. In addition, there are endemic species on the bank islands (Round Island) which are not known today or in the past on Mauritius, but which have probably either evolved *in situ* or are relict populations of species no longer extant on Mauritius, i.e., the gecko *Phelsuma guentheri* and the monotypic boiid genus *Bolyeria*.

These data strongly suggest that extinction among the endemic reptiles of the Mauritius bank has been greater on the main island than on the bank islands. The reasons for this differential extinction are unknown, but it is perhaps significant that a dramatic differential alteration of the ecology of these islands took place when man and his animals arrived and colonized the main island of Mauritius but, until quite recently, left the small bank islands relatively undisturbed. The case is unproved as yet, but man and his animals have already been deeply implicated in the extinction of the Mauritius birds, and their guilt may be equally great when the case of the reptiles comes to trial.

Pamelaescincus new genus[1]

Type species. Scelotes gardinieri Boulenger, 1909, Trans. Linn. Soc., ser. 2, Zool., vol. 12, p. 298.

Diagnosis. Similar to *Gongylomorphus* and the following genus and differing from all other scincine skinks in having the palatines and palatal rami of the pterygoids meeting medially to form a broad secondary palate (Fig. 7), and in having 11, instead of 10 or fewer, premaxillary teeth.

Among the Seychelles and Mauritius scincines, which appear to be the genus' closest relatives, *Pamelaescincus* is most similar in palatal characters to *Gongylo-*

[1] The genus is named after Pamela, the older of my two sisters.

morphus, but differs from this monotypic Mauritius genus in lacking both the frontoparietal scales and the clear spectacle in the lower eyelid.

Pamelaescincus is similar to other Seychelles scincines in lacking frontoparietals (which all other subsaharan Africa and Madagascar scincines have) and in having scaly eyelids; but differs from these species in lacking the posterior emargination of the palatal rami of the pterygoids (Fig. 7), in having 5 instead of only 4 fingers, and in having a high midbody scale count (30 to 34 instead of 22 to 24).

Distribution. The single species in the genus is reported from the following islands in the Seychelles archipelago: Mahé, Praslin, Silhouette, and Frigate.

*Species. Gardinieri** Boulenger, 1909.

Janetaescincus[1] new genus

Type species. Scelotes braueri Boettger, 1896, Zool. Anz., vol. 19, p. 349.

Diagnosis. Similar to *Gongylomorphus* and *Pamelaescincus* and differing from all other scincines in having the palatines and palatal rami of the pterygoids meeting medially to form a broad secondary palate (Fig. 7); and in possessing 11, instead of 10 or fewer, premaxillary teeth.

In skull morphology *Janetaescincus* differs from *Gongylomorphus* and *Pamelaescincus* in having the palatal rami of the pterygoids emarginated posteriorly (Fig. 7). On the basis of external characters the new genus is easily distinguished from *Gongylomorphus* and *Pamelaescincus* by means of its lower midbody scale count (22 to 24 instead of 30 to 38), and by the possession of only 4 fingers instead of 5. *Janetaescincus* also lacks the frontoparietals and clear spectacle in the lower eyelid of *Gongylomorphus*. The circular external ear opening is relatively smaller in *Janetaescincus* than in *Pamelaescincus* and, of course, is easily distinguishable from the horizontal slit in *Gonglyomorphus*.

[1] The genus is named after Janet, the younger of my two sisters.

Distribution. The two species of *Janetaescincus* are recorded from the following islands in the Seychelles: Mahé (*braueri*), Frigate (*veseyfitzgeraldi*), and Silhouette (both species).

*Species. Braueri** Boettger, 1896; *veseyfitzgeraldi* Parker, 1947.

SCINCINES OF MADAGASCAR

Too little is known about the skull morphology of Malagasy scincines to make any formal taxonomic decisions on this basis. Enough is known, however, to bring out the broad relationships between the scincines of Madagascar and the scincines of subsaharan Africa and the islands of the west Indian Ocean.

The single external feature that is shared by all Malagasy scincines and that serves to align them with certain other groups of scincines is the small interparietal scale. In the Malagasy species, as in *Proscelotes* and *Sepsina* in Africa, *Gongylomorphus* on Mauritius, and *Pamelaescincus* and *Janetaescincus* on the Seychelles, the interparietal does not touch the supraocular scales, and, of course, as in all scincines south of the Sahara and on the islands of the west Indian Ocean, except for *Gongylomorphus*, there are no frontoparietal scales.

Although the skulls of only a very few species of Malagasy scincines have been examined (see Specimens Examined section of paper), those skulls and *in situ* palates that have been examined show certain broad similarities. For instance, the palatines and palatal rami of the pterygoids do not meet medially in any of the skulls examined, and the palatal rami of the pterygoids are not expanded medially nor are they emarginated posteriorly. In other words, the palate is simple and is most similar to that of *Proscelotes* and *Scelotes*.

Most of the skulls of Malagasy scincines examined also have a separate and well-developed postorbital bone similar to the postorbital bone in *Proscelotes*, *Sepsina*, *Gongylomorphus*, *Pamelaescincus*, and *Janetaescincus*, that is, those genera with a

small interparietal not touching the supraocular scales.

In a very general way, therefore, the relationships of the Malagasy scincines seem to be closest to the African *Proscelotes* and *Sepsina* and the west Indian Ocean island genera *Gongylomorphus*, *Pamelaescincus*, and *Janetaescincus*. The strongest evidence at hand for this broad relationship is the small size of the interparietal scale and the well-developed postorbital bone in these skinks. Admittedly this seems to be thin evidence, but it is at present all we have to go on.

EVOLUTION AND ZOOGEOGRAPHY OF THE SUBSAHARAN AFRICA, SEYCHELLES, AND MAURITIUS SCINCINAE

Evolution

It is evident from the discussion above that three major groups of scincines are recognizable in subsaharan Africa, the Seychelles, and on the Mauritius bank. I wish to discuss the evolution of these three groups below.

(1) One of the three groups, the *Proscelotes-Sepsina* group, is the only taxon of subsaharan Africa scincines with a small interparietal which fails to touch the supraoculars. This is a primitive group in that the postorbital bone remains large and the supratemporal fenestra is open. In addition, *Proscelotes* retains the primitive digital formula of 5–5, and *Sepsina* is the only scincine in subsaharan Africa to retain pterygoid teeth. Both *Proscelotes* and *Sepsina* also seem to be much less closely adapted to a burrowing way of life than are many *Scelotes* and all *Melanoseps*, *Typhlacontias*, and *Scolecoseps*. It is impossible at this point, however, to say that either genus, *Proscelotes* or *Sepsina*, is more primitive than, and possibly ancestral to, the other. *Proscelotes* retains pentadactyl limbs (primitive), but lacks pterygoid teeth (advanced); whereas *Sepsina* has reduced the number of digits to 4–4 or fewer (advanced), but retains pterygoid teeth (primitive).

(2) The genera *Scelotes*, *Melanoseps*, *Scolecoseps*, and *Typhlacontias* seem to form another tightly-knit taxon immediately recognizable on the basis of the large interparietal, which is in contact with the supraocular scales. The group seems to have adopted a more secretive, subterranean way of life than have *Proscelotes* and *Sepsina*, and many of the adaptations to this way of life, as well as other less obvious adaptations of *Melanoseps*, *Scolecoseps*, and *Typhlacontias*, can be seen as trends within *Scelotes*. Some of the trends in *Scelotes* which appear to portend the adaptations of the other three genera are discussed below.

Loss of limbs: The species of *Scelotes* show various stages of limb and digit reduction from the primitive five-fingered, five-toed condition to the complete loss of all external traces of limbs (Table 1). All species of the other three genera except for *Typhlacontias brevipes*, which retains a single styliform hindlimb, are entirely limbless.

Loss of external ear opening: Roughly correlated with the loss of the limbs in *Scelotes* is the reduction in size and, ultimately, the loss of the external ear opening (Table 1). *Melanoseps*, *Scolecoseps*, and *Typhlacontias* also lack an external ear opening.

Fusion of supranasals: Although all species of *Scelotes* have paired supranasals which meet directly behind the rostral, some populations of *S. bipes* have these scales fused in a high proportion of the individuals. The fusion of the supranasals results in a single band-like scale behind the rostral, which is reminiscent of the single transversely enlarged "internasal" scale of *Typhlacontias*. *Melanoseps* and *Scolecoseps*, however, have the primitive paired supranasals of *Scelotes*.

Articulation of stapes and quadrate: In all the skulls of *Melanoseps*, *Scolecoseps*, and *Typhlacontias* examined (see Specimens Examined section), the bony shaft of the stapes is short and stout and projects posterolaterally to articulate directly with

a ventrally projecting nub from a posterior extension of the quadrate. The same relationship between the stapes and quadrate is also seen in *Scelotes arenicolor*, while a very close approximation to the *Melanoseps*, *Scolecoseps*, *Typhlacontias* condition (stapes abuts quadrate obliquely) can be seen in *Scelotes caffer* and *S. anguina*. Other species of *Scelotes*, however, have the more usual stapes-quadrate relationship in which the relatively more slender and longer stapes is directed laterally and articulates with the tympanum via cartilage. From the few skulls of *Scelotes* examined, there appears to be little correlation among the relationships of the stapes and quadrate, and the degree of loss of the digits, and the reduction in size of the external ear opening.

Reduction and loss of the postorbital bone: In *Scelotes* there is a tendency to reduce and ultimately lose the postorbital bone (Table 1), and in *Melanoseps*, *Scolecoseps*, and *Typhlacontias* the postorbital is lacking altogether. Even in its most well-developed condition in *Scelotes*, the postorbital bone is generally smaller than in *Proscelotes* and *Sepsina*.

Obliteration of supratemporal fenestra: Whereas the supratemporal arch is strong and the supratemporal fenestra well developed in *Proscelotes* and *Sepsina*, the arch is weak and the fenestra, at best, small in some *Scelotes*. In the remaining *Scelotes* and in *Melanoseps*, *Scolecoseps*, and *Typhlacontias* the fenestra is obliterated entirely by the close apposition of the postfrontal, postorbital (when present), and squamosal bones with the parietal.

Although it is fairly clear that *Melanoseps*, *Scolecoseps*, and *Typhlacontias* are relatives of *Scelotes* and probably share a common ancestry with *Scelotes*, the relationships of the taxa are not entirely clear. *Melanoseps* differs morphologically from *Scelotes* only in showing posterior emarginations of the palatal rami of the pterygoids, and *Scolecoseps*, in turn, differs from *Melanoseps* primarily in having the external naris situated well forward in the large rostral scale. The sequence *Scelotes* → *Melanoseps* → *Scolecoseps* would be a reasonable morphological sequence by which to explain the evolution of these taxa. *Typhlacontias*, on the other hand, with its one species (*brevipes*) with a styliform hindlimb, may have evolved independently from a *Scelotes*-like ancestor.

(3) Finally, a third group, whose genera have been discussed in a formal systematic manner above, consists of the monotypic Mauritius *Gongylomorphus*, and the two genera (3 species), *Pamelaescincus* and *Janetaescincus*, on the Seychelles. The osteological similarities which align these skinks (11 premaxillary teeth, complete secondary palate involving both the palatines and pterygoids, large postorbital bone, and supratemporal fenestra) are striking and to me indicate close relationship instead of convergence. *Gongylomorphus* appears to be more primitive than *Pamelaescincus* and *Janetaescincus* in retaining a pair of frontoparietals scales, and *Pamelaescincus*, in turn, appears to be more primitive than *Janetaescincus* in lacking the posterior emarginations on the palatal rami of the pterygoids and in having 5 instead of 4 fingers.

Zoogeography

I now would like to make two very general comments about the zoogeography of the groups discussed above. First, if the size of the interparietal scale, i.e., whether it touches the supraocular scales or not, is truly indicative of relationship within the scincines of subsaharan Africa, Madagascar, and the west Indian Ocean islands, then we have two major groups with highly suggestive distributions. On the one hand, the scincines with the small interparietal are widely distributed throughout the area, whereas the scincines with the large interparietal are confined to continental Africa. Simply on the basis of the distribution of these two groups, it would be reasonable to argue that the more widespread group, i.e., the group that occurs on Africa, Madagas-

ear, and the islands of the west Indian Ocean, probably appeared in the area before the group that occurs only on the African mainland.

This interpretation has the support of the morphological data. The large interparietal of *Scelotes*, *Melanoseps*, *Scolecoseps*, and *Typhlacontias* is unusual in skinks and is probably derived from the small interparietal condition. The reduction and loss of the postorbital bone and the predominate trend toward burrowing habits in this group also imply its specialized evolutionary role. This evidence suggests that perhaps the large interparietal line evolved on continental Africa from the more widespread and less specialized small interparietal line.

The second zoogeographic point I wish to make cornerns the Seychelles and Mauritius scincines. The single Mauritius genus (*Gongylomorphus*) and the two Seychelles genera (*Pamelaescincus* and *Janetaescincus*) appear to be each others closest relatives. There is a problem, however, in explaining how such closely related taxa can occur on two remote and widely separated oceanic island banks. The easiest explanation for this distribution might be that the three genera are simply relicts from a group of scincines that were once much more widely distributed over Africa and/or Madagascar. The flaw in this argument, however, is the notion that the complete secondary palate which unites the Mauritius and Seychelles scincines seems to be an extremely advanced character and is in no way primitive. That is, the complete secondary palate of these scincines appears to be an innovation unique to the scincines of the islands, and as the island banks were probably never connected in the past, skinks with this palatal character must have first appeared on one island bank and then dispersed over water to the second island bank.

The most likely method of over water dispersal for these skinks is by rafting. The probability of successful rafting is greatly increased by the availability of large rivers to carry detritus out to sea, but at present neither the Seychelles nor Mauritius seems to offer a favorable source of rafts. In the recent, and perhaps more distant past, however, this was not the case. Whereas the volcanic Mauritius bank is relatively small (only slightly larger than the main island itself) and rises from very deep water, the largely granitic Seychelles lie on a very shallow, but relatively extensive (approximately 12,000 square miles), bank and would probably form "an extensive, low archipelago" with the standard Pleistocene lowering of sea levels. Under these circumstances large tropical rivers may have existed in the Seychelles and would perhaps have greatly increased the probability of dispersal from the Seychelles to Mauritius. If this were the direction of dispersal, we might visualize the primitive *Gongylomorphus* or its ancestor rafting from the Seychelles to Mauritius and surviving there as a relict while the parental stock became extinct on the Seychelles but was represented by the derived *Pamelaescincus* and *Janetaescincus*.

A KEY TO THE SCINCINE GENERA OF SUBSAHARAN AFRICA

Interparietal scale not touching supraocular scales; postorbital bone present and well developed.
- Digital formula 5–5; pterygoid teeth lacking ..... *Proscelotes*
- Digital formula 4–4 or lower; pterygoid teeth present ..... *Sepsina*

Interparietal scale touching supraocular scales; postorbital bone present but only weakly developed, or lacking entirely.
- A single postrostral scale (fused supranasals); jugal bone lacking; 5–6 maxillary teeth ..... *Typhlacontias*
- A pair of postrostral scales (supranasals); jugal bone present; 10–23 maxillary teeth.
  - External naris well within an enlarged postrostral ..... *Scolecoseps*
  - External naris near or bordering posterior edge of rostral scale.
    - Palatal ramus of pterygoid bone deeply emarginated posteriorly (Fig. 5) ..... *Melanoseps*
    - Palatal ramus of pterygoid bone smoothly diverging along its posteromedial edge (Fig. 4) ..... *Scelotes*

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The brunt of the skeletonizing that was necessary for this paper has been borne by the herpetological collections of the Museum of Comparative Zoology (MCZ). Dr. Ernest E. Williams, as curator of that collection, has been extremely generous in making the collection available to me and has gone far in helping me obtain specimens not in the museum collections. The following people have provided the "crucial" specimens needed for this paper: Mr. Charles M. Bogert and Dr. Richard G. Zweifel of the American Museum of Natural History (AMNH); Miss A. G. C. Grandison of the British Museum of Natural History (BM); Dr. Robert Inger and Mr. Hymen Marx of the Field Museum of Natural History (FMNH); Monsieur Jean Guibé of the Muséum National d'Histoire Naturelle (MNHN); Dr. James A. Peters and the late Dr. Doris Cochran of the United States National Museum (USNM).

Dr. E. E. Williams has read the paper and offered several helpful criticisms. In addition, part of the work for this paper was supported by funds from NSF grant GB 6944 to Dr. Williams.

SPECIMENS EXAMINED

I have seen the following complete skulls:

GONGYLOMORPHUS: *bojeri* MCZ 46677.

GRANDIDIERINA: *lineata* MNHN 3378.

JANETAESCINCUS: braueri BM 1910.3.18.33.

MELANOSEPS: ater MCZ 50955, 52487; *occidentalis* BM 1907.5.22.6A.

PROSCELOTES: aenea MCZ 18709; *arnoldi* MCZ 55145; *eggeli* MCZ 24217, 24218, 24220.

PAMELAESCINCUS: gardinieri BM 1910.3.18.91.

PYGOMELES: *braconnieri* MNHN 1715.

SCELOTES: anguina MCZ 96791; *arenicolor* MCZ 14205; *bidigittata* MCZ 96789; *bipes* BM XVII.2.F; *brevipes* MCZ 21237; *caffer* MCZ 96792; *gronovi* BM 97.5.15.8; *limpopoensis* MCZ 96906; *mira* MCZ 96790; *ulugurnensis* MCZ 24206.

SCOLECOSEPS: *boulengeri* MCZ 18357.

SEPSINA: angolensis FMNH 142793, AMNH 40734; *bayoni* BM RR 1967.80; *tetradactyla* MCZ 42885, 47770 (3 specimens), 47775, 56963, 56965, 56967, 85536.

TYPHLACONTIAS: brevipes MCZ 96702; *gracilis* USNM 159338; *ngamiensis* FMNH 142787, 142791 (cleared and stained specimen).

VOELTZKOVIA: mira MCZ untagged specimen.

Malagasy *incertae sedis* "*Scelotes*": *astrolabi* MCZ 20953; *melanura* MCZ 11733; *splendidus* FMNH 72086.

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Studies on the Fossil Snake *Dinilysia patagonica* Woodward: Part I. Cranial Morphology

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STUDIES ON THE FOSSIL SNAKE *DINILYSIA PATAGONICA* WOODWARD: PART I. CRANIAL MORPHOLOGY

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ABSTRACT

A snake fossil described in 1901 by Sir Arthur Smith Woodward and named *Dinilysia patagonica* is significant not only because of late Cretaceous age but because it is essentially a complete specimen. It was recovered from sandstone deposits near the Río Neuquén, Chubut Territory, Argentina. Relatively little notice has been accorded this significant fossil, primarily because it was incompletely prepared. Since many significant features of the specimen were thereby concealed, Woodward described *Dinilysia* as "a typical member of the Order Ophidia" and related it to the modern burrowing snake *Anilius* (=*Ilysia*). The present study indicates that he was mistaken in the first of these statements but at least partially correct in the second.

The following snakelike characters are present: (1) prokinetic skull, (2) loss of both temporal arches, (3) ventral enclosure of brain by frontal and parietal bones, (4) loose articulation of dentary with posterior mandibular bones. Other snake resemblances also occur, and the skull has a distinctly snakelike appearance.

The lizardlike (or primitive) characters are more numerous than those present in modern snakes. The most striking are (1) palatine bones that are deeply channeled for the internal choanae and that lack the anterior toothed projections of modern snakes, (2) presence of a jugal bone, (3) presence of both postfrontal and postorbital bones, the latter contacting the jugal as shown on the original cast of the specimen, but now broken on the fossil, (4) single trigeminal foramen, (5) pterygoid bones vertical posteriorly, (6) a single opening in the front of the braincase for olfactory tracts, (7) stapedial footplate not enclosed by a crista circumfenestralis, (8) large, laterally-projecting basipterygoid processes.

Unusual or unique features of *Dinilysia* are the robust nasal septum, the vomers underlain by palatines, the low position of the fenestra rotunda on the occiput, the peculiar shape of the jugals, the deeply-grooved transverse suture between parasphenoid and basioccipital, and both the size of the paroccipital process and the relatively large supratemporal bone. The peculiar oval jaw joint is unique and unlike both the strongly saddleshaped articulation of snakes and the similar but less extreme joint of lizards.

Characters in *Dinilysia* that show resemblance to the modern aniliid snakes are: (1) the large paroccipital processes, (2) the dorsal exposure of the prootic as a tiny sliver surrounded by parietal, supratemporal, supraoccipital, and exoccipital bones, (3) the shape of the supraoccipital, (4) the large stapes, (5) the broad attachment of the quadrate bone to the paroccipital process, (6) the wide, *Cylindrophis*-like cultriform process of the parasphenoid.

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The lizardlike characters do not relate *Dinilysia* to any particular group of lizards; indeed most of the characters are probably generalized lepidosaurian features. Some aspects of the occiput and the palate (especially the posterior palatine and pterygoid region) resemble those of the Recent platynotan *Lanthanotus*, but there are also non-platynotan resemblances, such as the depth of the choanal impressions on the palatines.

Dinilysia is a mosaic, but in spite of its lizardlike features it is clearly a snake and shows detailed resemblances to the modern Aniliidae that cannot be dismissed as convergent. These modern forms are probably the closest relatives of *Dinilysia* among living snakes, and the unique features do not seem fundamental enough to weaken this relationship. *Dinilysia* should be placed in a family separate from the Aniliidae, and probably belongs at the base of the superfamily Booidea.

INTRODUCTION

Fossil snake remains tend to be both infrequent and fragmentary. The majority of snake fossils consist of vertebrae and ribs, parts that, although furnishing certain characters of interest to systematists, are quite strikingly similar from group to group. Few snake skulls have been preserved as fossils and, thus, this greatest potential source of information pertinent to the phylogeny of the Serpentes has been all but wanting.

It is thus remarkable that one of the very oldest known fossil snakes, *Dinilysia patagonica* Woodward (1901) from the Upper Cretaceous of South America, is excellently preserved and includes a nearly complete skull, mandibles, and many vertebrae. Such a specimen might be the focal point of all speculations on the origin and early evolution of the snakes, but, despite considerable interest in snake ancestry (see especially Bellairs and Underwood, 1951; McDowell and Bogert, 1954; Underwood, 1957), *Dinilysia* has received little more than mention. This is not altogether surprising; Woodward's original description of *Dinilysia* is brief and draws attention to few characters that are not present in many living snakes. Woodward underlined this rather unexciting portrayal of almost the oldest fossil snake with the statement that, on the basis of cranial structure, *Dinilysia* is "a typical member of the order Ophidia" (1901: 178).

We have had the opportunity to reexamine the skull of *Dinilysia*, and further preparation by one of us (RE) has exposed the palate for study. We are unanimous in our opinion that *Dinilysia* is *not* a "typical" snake, and that it possesses both specialized and primitive features so far unknown in other snakes. It is our aim, here, to redescribe what seems to us the most important fossil snake yet discovered and to note some of the ways in which *Dinilysia* resembles other members of the Squamata. We hope in this way to place *Dinilysia* in its proper context and to enable it to be discussed intelligently in relation to the origin and early evolution of snakes. We do not, however, propose such a discussion here. It is evident to us that further advances in the study of snake origins will require the study of primitive living snakes in more meticulous detail than is found in any work now available, and definitive conclusions may require the discovery of critical fossils still unknown.

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The manuscript has been read critically

by Dr. Samuel B. McDowell (Rutgers, The State University, Newark, New Jersey), Dr. Garth Underwood (Sir John Cass College, London) and Dr. Thomas Parsons (University of Toronto). We have found their suggestions very helpful although we alone accept responsibility for the accuracy of the interpretations offered herein.

Mr. Anthony Laska made excellent casts of the skull; these are the more remarkable when the soft and delicate condition of the fossil is considered. Figures 5–12 were prepared by Mr. László Meszoly, and the photographs were made by Mr. Fred Maynard of Boston University.

We are grateful to a number of sources for financial aid during the course of this project. An American Philosophical Society Grant No. 3665 to Estes made possible preparation and some of the illustrations, and his research time was supported in part by National Science Foundation grants GB-1683, GB-4303 and GB-7176. Travel and research time for Frazzetta was provided in part by his National Institutes of Health Postdoctoral Fellowship during 1964–65 and his N. S. F. grant GB-5831. The Milton Fund of Harvard University supported the preparation of some of the figures.

THE GEOLOGICAL OCCURRENCE AND PRESERVATION OF THE SPECIMEN

The unique specimen of *Dinilysia patagonica* consists of an articulated skull, jaws, and most of a vertebral column. It is preserved in a reddish brown sandstone that contains a high percentage of clay-sized particles cementing the medium sand grains. It was recovered from the sandstone deposits near the Río Neuquén, Chubut Territory, Argentina (Feruglio, 1949). These widespread late Cretaceous sediments were laid down following a great marine transgression in southern South America and are bounded above and below by strata bearing plant and animal fossils of characteristic late Cretaceous aspect; the age of the specimen is thus unquestionable. The deposits seem to have been formed on a flood plain; in this and their relationship to marine transgressions they resemble many North American late Cretaceous deposits formed under a similar regime.

The associated fauna includes giant horned turtles and large carnivorous dinosaurs.

The preservation of the bone is excellent; it is white when newly prepared and resembles Recent bone. Unfortunately, it is also chalky and brittle and does not absorb protective substances such as Alvar or Glyptal readily.

The skull and jaws are little eroded except at the terminal snout region. Some of the materials used in the past to protect the specimen have resulted in damage over the years: shellac has dried, shrunk and exfoliated some of the surfaces, and mastic, a soft waxy substance (in part beeswax) used to fill some crevices, has permeated the surrounding bone, making it cheesy in texture and difficult to preserve.

There is little, if any, distortion or crushing evident. The chief agent that has disturbed the specimen is weathering, most of which seems to have been post-depositional and subaerial. A large pre-depositional crack extends across the right temporal process and is the only instance of crushing significant enough to warrant comment. As a result, the process itself is depressed below the dorsal skull level and separated from the dorsal skull table by a broad, matrix-filled area. A fragment of bone, probably a part of the prootic in the region of the above-mentioned crack, lies on the right pterygoid. There is apparently no distortion of the individual bones; only a simple dislocation seems to have occurred.

As originally preserved (Plates 1 and 2) the jaws were agape, and the elements of the right mandible were almost separated and bent at an unnatural angle. This indicates that some maceration had probably occurred before burial, but not sufficient to disarticulate the specimen.

Unfortunately, the most serious damage to the specimen has been suffered since the entrance of *Dinilysia* into the literature. The most important such changes are the breakage and loss of parts of the maxillae, the postorbital bar, and the loss of the left dentary region. These are discussed in more detail under the sections on the respective bones. We regret to say that there has been additional damage to the specimen during this study as a result of the very brittle nature of the bone. The posterior end of the right dentary with the splenial is now missing. The right postdentary bones have lost some bone dorsally. The right maxilla has been badly cracked posteriorly and some bone lost on the dorsal surface. Preparation of the skull necessary to study important features has resulted in many minor breakages. The snout region was broken and repaired with minor loss of bone and slight dislocation of elements after the casting of the specimen. Fortunately almost all of the above damage has been suffered subsequent to photographing (except Plate 5 of the occiput), illustration and casting. Thus the figures represent the specimen at its best while available to us.

A cast of the specimen as it was during Woodward's description is in the British Museum (Natural History). Dr. Alan Charig has very kindly had this copied for our study and states that the copy faithfully reproduces the original *cast*. Two views of the copy are figured here as Plate 2. Unfortunately, the original cast does not give more than the gross shape of the specimen, but it does allow some questions about the original specimen to be discussed: the number of maxillary and dentary teeth, the original extent of the maxillae, and the extent of the postorbital bar. These will be discussed in the appropriate sections.

We repeat below Woodward's original description; his figures (1a, 1b, 1c of his plate XX) are reprinted here as Plate 1. We do this (1) because the views expressed by Woodward are of interest; (2) because this is a report on the specimen before it suffered the damage that has resulted in its present diminished condition; and (3) because reproduction of Woodward's description in itself provides the reader with all previous substantive literature dealing with this fossil: other than the diagnosis of the family Dinilysiidae given by Romer (1956: 570), there have been no citations that are not mere mentions (or abstracts of this study; Estes, 1966; Estes et al., 1966).

> "II. An Extinct Ophidian, *Dinilysia patagonica*, gen. et sp. nov. (Plate XX.)
>
> "Mr. Roth's discovery of a fossil Ophidian in the red sandstone of Nequén, associated with typical Mesosuchian Crocodiles, has already been recorded,[2] but the unique specimen referred to has not hitherto been studied. It comprises the greater part of the skull and mandible, and fragmentary remains of the anterior half of the vertebral column; the cranium being in an especially good state of preservation.
>
> "The skull (Plate XX, figs. 1, 1a) is long, narrow, and depressed, with the cranial region as long as the facial region. It seems to have been widest at the occiput, where the otic region is very massive; and the maximum compression is immediately in front of this, where the parietals rise into a prominent sagittal crest. The constitution of the hinder part of the skull is best seen on the left side of the fossil, where there is only one slight antero-posterior crack (*x*) in the bones. The right postero-lateral angle, on the other hand, is fractured and displaced downwards. The foramen magnum, which is filled with matrix, is completed above by the exoccipitals (*ex.occ.*), which meet in the middle line. They are directly continuous on each side with a great, expanded piece of bone (*op.*), which curves backwards as well as outwards and abuts upon the bone at the upper end of the quadrate. This expansion of the exoccipital is probably the opisthotic, which is similarly fused with the exoccipital in Lacertilia and the extinct Mosasaurs. Above the exoccipitals is the short but laterally-extended supraoccipital (*s.occ.*), which completes the sagittal crest behind. Its lateral extremity on the left is in contact with a small trace of bone (*o.*), which is exposed between the opisthotic, parietal, and the bone

[2] A. Smith Woodward, Anales Mus. La Plata —Paleont. Argent. no. iv (1896), p. 1.

at the upper end of the quadrate. The fragment is doubtless the highest point of the anterior otic bone, of which the upper part is otherwise completely buried by the surrounding elements. The parietals (*pa.*) occupy nearly half the entire length of the cranium, curve downwards to form the side walls, are much compressed in their anterior two-thirds, and rise into a conspicuous sagittal crest. They are flattened in the middle line at their anterior end, and are not pierced by a pineal foramen. Each of the frontals (*fr.*) is nearly three times as long as broad, and slightly widest at its truncated anterior end. There is no supra-orbital bone; but posteriorly and anteriorly the outer border of the frontal is slightly notched for the accommodation of the postfrontal and prefrontal respectively. The postfrontal (*pt.f.*) seems to have partly bounded the comparatively small orbit (*orb.*) behind; but this bar is broken away on both sides. The prefrontal (*pr.f.*), best preserved on the left (fig. 1a), is flattened and triangular in shape, almost equilateral; it is only slightly in contact with the postero-lateral angle of the nasal bone. The nasals (*na.*) are also flattened and triangular in shape, but antero-posteriorly elongated and with a somewhat concave outer side which bounds the relatively large narial opening (*nar.*). They are widest at their articulation with the frontals. They are incomplete in front, and the premaxillae are unfortunately not shown. The greater part of the palate is obscured by matrix or broken away, but some features at the postero-lateral angles of the cranium and in the facial region are well shown. As observed especially on the left side (fig. 1), a long and narrow plate of bone (*s.t.*) forms the postero-superior boundary of the parietal and otic region, and seems to constitute the articulation for the quadrate. This is doubtless the element commonly named supratemporal in Snakes, Lizards, and Mosasaurs. The quadrate (*qu.*) is evidently short and broad, but is only imperfectly shown in section on the left side. Its remains (Pl. XX, fig. 1c) are not readily interpreted; but the upper end of the bone seems to be displaced outwards and incomplete in the fossil, while the more expanded lower end shows the large notch which usually forms a loose articulation for the pterygoid in Snakes. At first sight, it might be supposed that the quadrate was of the same form as that of the Mosasaurs, with a deep posterior notch for the auditory meatus; but closer study seems to make this interpretation impossible. At the side of the cranium, below the supratemporal and parietal, the upper border of a large prootic (*pr.o.*) is exposed; while between this bone and the orbit the downwardly curved portion of the parietal forms a sharp longitudinal lateral ridge (*r.*). There are no traces of temporal arcades. The short pterygoids (*pt.*) are partly exposed, and a portion of the palatine below the orbit on the left side bears traces of two comparatively minute teeth. There are distinct remains of an ectopterygoid or transverse bone (*ec.*) on each side between the pterygoid and maxilla; and a fragment on the left side seems to show that this element overlapped the maxilla to a considerable extent. The maxilla itself (*mx.*) is relatively large, and best preserved on the right side. It is stout and curves inwards in front. It articulates not only with the pterygoid behind by the intervention of the transverse bone, but also with the palatine by a broad articular palatal process which extends inwards from its middle. It likewise articulates directly with the prefrontal in an extensive suture. It shows 14 or 15 large shallow sockets for the implantation of teeth (fig. 1b); and one dental crown preserved at the hinder end of the left maxilla is very slender and recurved. The fragmentary remains of the mandible show it to have been of the usual slender ophidian type, with a very loose articulation between the dentary (*d.*) and articulo-angular region (*ag.*); and the dentary exhibits a series of large shallow tooth-sockets like those of the maxilla.

"Behind the skull there are remains of a long series of typical ophidian vertebrae, which do not present any features worthy of special note. The neural arches are shown to have borne delicate low spines, though nearly all of these have been broken away and are only represented by their bases in the fossil (Plate XX, fig. 2, *n.*). The ribs (*r.*) are very stout.

"From this description it is evident that the Patagonian fossil in question represents a typical member of the order Ophidia. As shown, however, by the conformation of the occiput and the relatively small size of the quadrate, it belongs to one of the more generalized types. Its closest allies may therefore be sought among the Boidae and Ilysiidae, which still constitute so large and characteristic a part of the Ophidian fauna of South America. The skull bears much general resemblance to that of a *Boa constrictor*, but is readily distinguished from the latter by its non-projecting supratemporal and relatively small quadrate. It is similarly distinguished from the skull of all the other Boidae.[1] In precisely this character,

[1] G. A. Boulenger, Catalogue of the Snakes in the British Museum (Natural History), vol. i (1893).

on the other hand, the fossil skull agrees with that of the existing Ilysiidae; and its occipital region is almost identical with that of the South American genus *Ilysia*.[2] The resemblance to the latter, indeed, is so close that, although the coronoid region of the mandible is not observable in the fossil, there need be little hesitation in referring the extinct type now described to the family Ilysiidae. It differs from the existing genera of the family in its more numerous marginal teeth and relatively smaller palatine teeth; in its elevated sagittal crest; and in the presence of well-developed neural spines on the vertebrae. It also differs from the South American *Ilysia*, though agreeing with the Javan *Cylindrophis*, in the possession of a small postfrontal bone. It may, in fact, be regarded as a comparatively gigantic forerunner of the Ilysiidae, analogous to *Glyptodon* among the Armadillos and *Phororhachos* among the Cariamas. Whereas the modern representatives of the family are small and degenerate burrowing snakes, the largest less than a metre in length, the extinct Patagonian snake, judging by the size of its vertebrae, must have attained a length of at least two metres. It had a relatively large head, and probably resembled the modern Boas in habit.

"This fossil evidently represents a hitherto unknown genus, which may be named *Dinilysia* and defined thus:- Marginal teeth of moderate size, about 14 or 15 in the maxillary series; palatine teeth relatively minute. Head rather large, the occipito-parietal region constituting half of the skull, with elevated sagittal crest; frontals longer than broad; small postfrontals present; prefrontals triangular, almost equilateral, only slightly in contact with nasals, which are long and narrow, tapering forwards. Vertebrae with low, delicate neural spines.

"The type species, of which remains are now described, may be named *D. patagonica*, and defined by the minor characters of the head-bones already noted."

Woodward's description of *Dinilysia patagonica* is not only short but unfortunately inadequate. Our major disappointment with Woodward's description is simple, though not trivial—Woodward stopped short of treating those characters that make *Dinilysia* both a unique animal and a significant discovery. This complaint applies to those parts that were exposed when Woodward examined the specimen as well as to those portions that were hidden and for which, of course, Woodward could not be held accountable. Woodward's failure to recognize the distinctive nature of *Dinilysia* might well have stemmed from the paucity of comparative material available to him. He mentions specific comparisons of *Dinilysia* with *Ilysia* (= *Anilius*) and also with *Boa constrictor*, but lists no other boiform genera by name. Perhaps with a larger collection of cranial material to hand Woodward might have been more able—or more confident—to identify certain features that set *Dinilysia* sharply apart from all other snakes. We attempt below to correct the deficiencies of Woodward's description.

A REDESCRIPTION OF THE CRANIAL REGION OF *DINILYSIA PATAGONICA*

General Features of the Skull

In general aspect, the skull is flat and broad anteriorly with the orbits opening dorsally as well as laterally (Figs. 1a–b and 3). Behind the level of the frontals the braincase becomes narrower and gracefully lengthened. Caudally the posterior braincase swells smoothly transversely to produce a pair of strong, posterolateral projections. A more detailed account now follows in which each bone is treated individually.

SNOUT COMPLEX

Premaxilla

Examination of the jagged cross section through the anterior ends of the nasals in *Dinilysia* reveals no indication of premaxillary structures. In addition, the copy of the original British Museum (NH) cast indicates that the maxillae extended close to the midline (see Plate 2). These facts might indicate that the premaxilla was of limited lateral and vertical extent were it not that, in many modern boids, the maxillae possess considerable freedom for transverse displacements. In some of these, the anterior

[2] G. A. Boulenger, *tom. cit.* (1893, p. 132, fig. 8.)

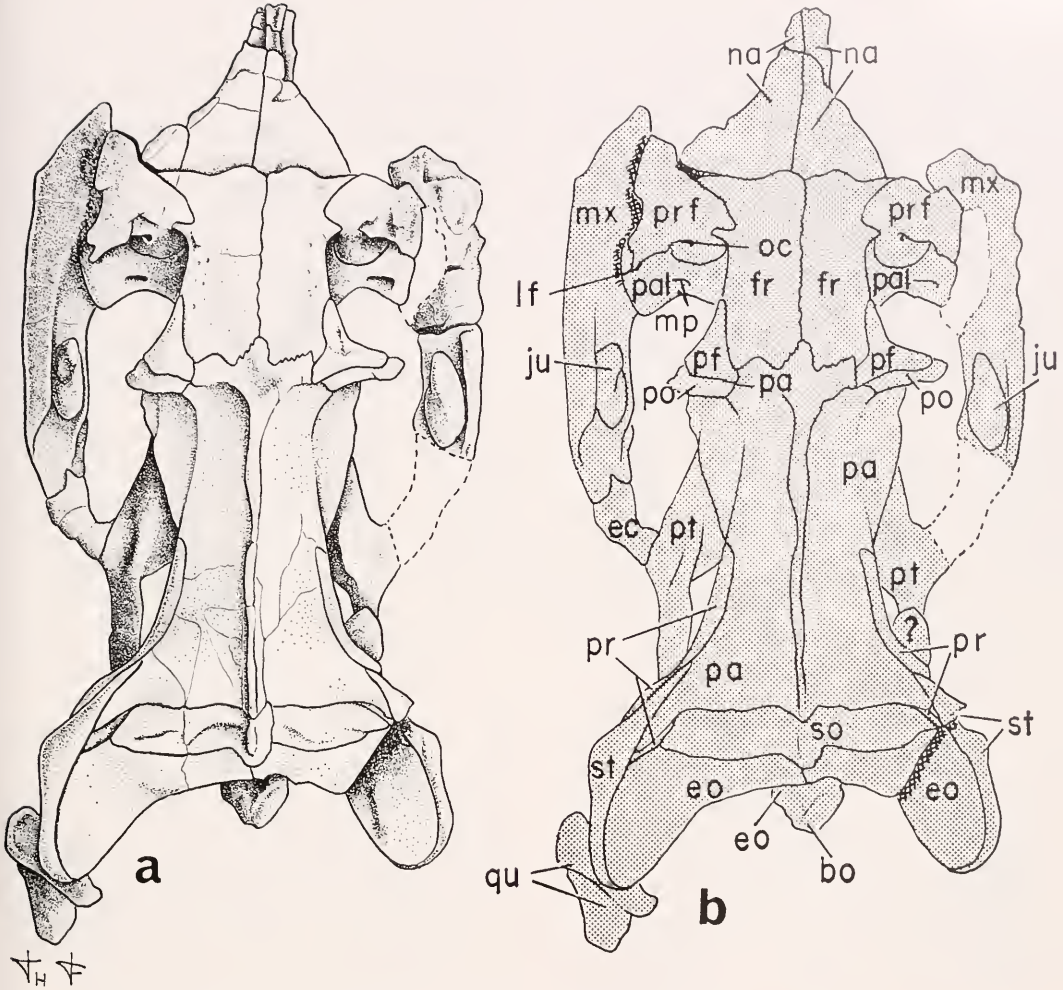


Figure 1. *Dinilysia patagonica*; dorsal view of skull. Abbreviations on p. 62. × 1.5.

maxillary tips can be brought fairly close to the cranial midline following removal of the premaxilla. Moreover, in certain boids with wide premaxillae (e.g. *Boa*, *Eunectes*), the premaxillary transverse process lies just in front of the tips of the maxillae.

Nasal

Figs. 1, 2a–b, 3, 7; na.

The paired nasals together form a nearly equilateral triangle in dorsal view whose anterior apex is displaced slightly to the right. The anteriormost portions of the nasals are badly eroded and incomplete. Originally, the posterolateral nasal corners extended to the lateralmost limits of the anterodorsal edges of the frontals to produce a wide zone of contact between these elements at the nasofrontal articulation (Fig. 1). The nasofrontal articulation is described below in the section on the frontal.

In lateral view, the nasals are relatively thick. Anteriorly, their inferior surfaces slope gently ventromediad and form a thickened internasal partition.

Septomaxilla

Figs. 2a–b, 3, 7; sm.

Although the snout region is broken, there is no real difficulty in interpretation

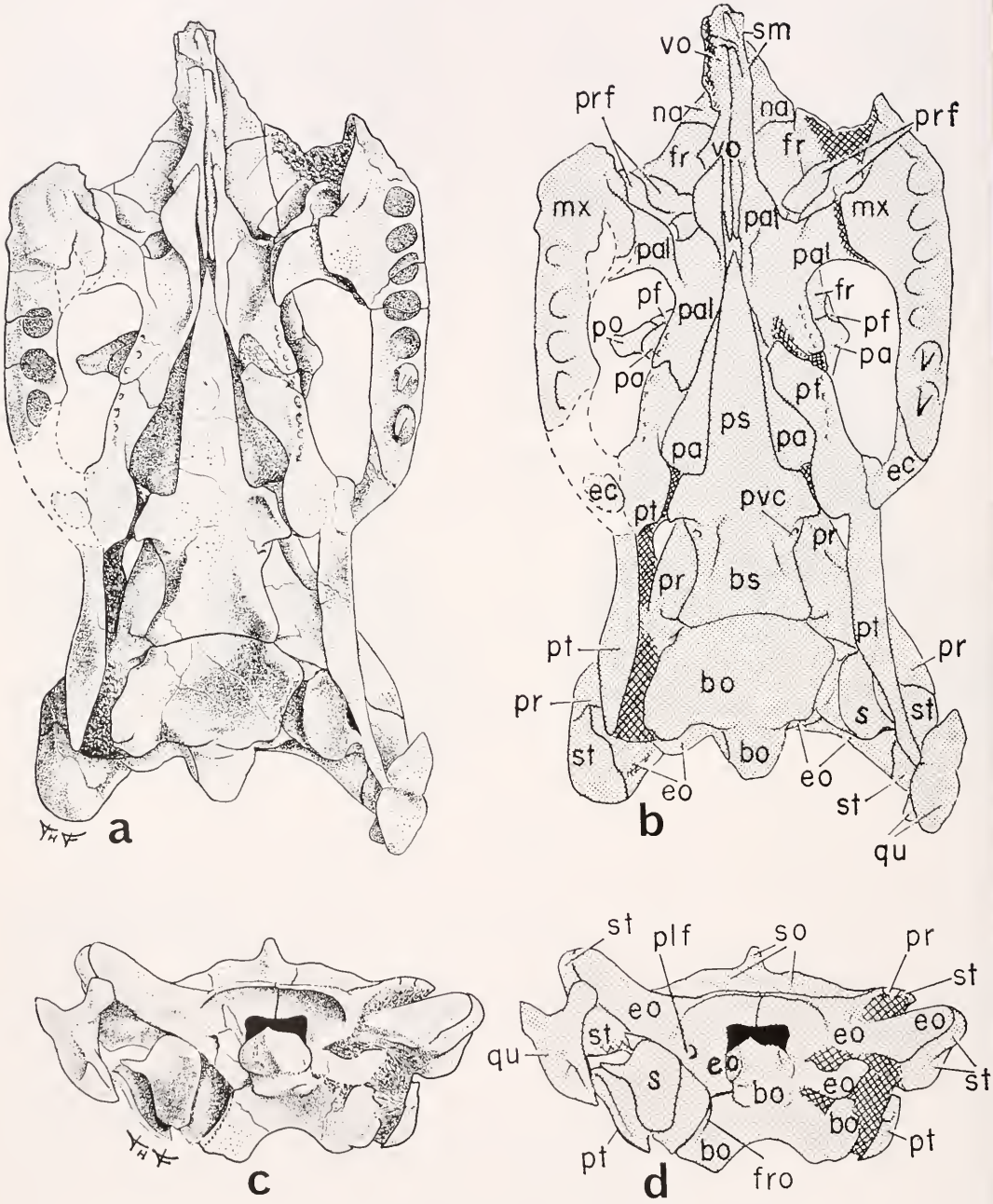


Figure 2. *Dinilysia patagonica*; ventral and occipital views of skull. Abbreviations on p. 62. × 1.5.

of the bone remnants. On the right side, a thin bony shelf extends along the anteroventral border of the nasal, beginning about 4 mm anterior to the nasofrontal contact. This shelf makes a gentle curve ventrally as it extends anteriorly, and its dorsal surface is inclined lateroventrally throughout its length. Anteriorly, the cross section through the snout (Fig. 7a) shows this plate of bone to be applied closely to bony fragments that appear to be continuous with the vomers (see below). On the left side, only a tiny bar of bone in the same position represents the septomaxilla. Posteriorly this fragment slopes dorsally away from the vomer, leaving space between them that must have housed the vomeronasal organ.

Vomer

Figs. 2a–b, 3, 7; vo.

Ventrally and posteriorly, the vomer meets the palatine at a somewhat indistinct junction. The junction is more easily discerned on the right where the palatine appears to extend forward as a flat, pointed process ventral to the vomer. On the left, however, a line of demarcation between the corresponding palatine and vomer is not clear.

Just anterior to the vomer-palatine junction on the right, the vomer is slightly widened laterally; medially and more posteriorly, the vomers are visible between the palatines as a pair of slender, rodlike processes (Figs. 2a–b), each of which is the ventral edge of a vertically oriented plate. Anteriorly the vomers are separated from their posterior portions by a matrix-filled crack. Their anteriormost portions directly underlie the septomaxillae (Fig. 7b).

BRAINCASE

Frontal

Figs. 1, 2a–b, 3; fr.

In dorsal view both frontals together are longer than wide and are separated by a longitudinal, very slightly irregular median suture. The upper surface of each is very gently convex anteromedially and bears a shallow concavity that is bounded medially by the convexity just noted, and laterally by a slightly raised frontal rim above the orbit. About six or seven tiny foramina extend in a crooked line along the medial slope of this rim. Posteriorly the frontals meet the parietal in a jagged transverse suture, while posterolaterally the frontals are indented by portions of the postfrontals.

Anterolaterally the upper surfaces of the frontals are joined by dorsal tonguelike processes of the prefrontal bones. Dorsally, these elements each appear to extend into a frontal notch that accommodates them so that the prefrontal surfaces are at the same level as those of the frontals. The adjacent edges of the dorsal prefrontal and frontal surfaces lie against one another and appear to be tightly connected. Each prefrontal is very slightly notched to receive the laterally projecting frontal edge. The notch horizontally divides the prefrontal into the dorsal tonguelike process just described, and a smaller ventral tonguelike process that is pressed against the lower surface of the frontal and is visible ventrally and posterolaterally (Figs. 2a–b).

Anterior to the prefrontal the dorsal frontal surface widens suddenly, transversely increasing the anterior frontal border as it meets the nasals.

A comparison between dorsal and ventral lines of demarcation separating the nasals and frontals reveals that, although the upper line is relatively straight and transverse, the lower line is shallowly V-shaped and lies from one (medially, at the apex of the V) to nearly five millimeters (about 30% of the total nasal length) in advance of the dorsal juncture (compare Figs. 1a with 2a, 1b with 2b). Examination of the lateral edge of the right nasal shows that posteriorly the nasal suddenly becomes vertically thinner where it lies upon an anteriorly projecting frontal shelf that underlaps it; the rostral borders of the paired frontal

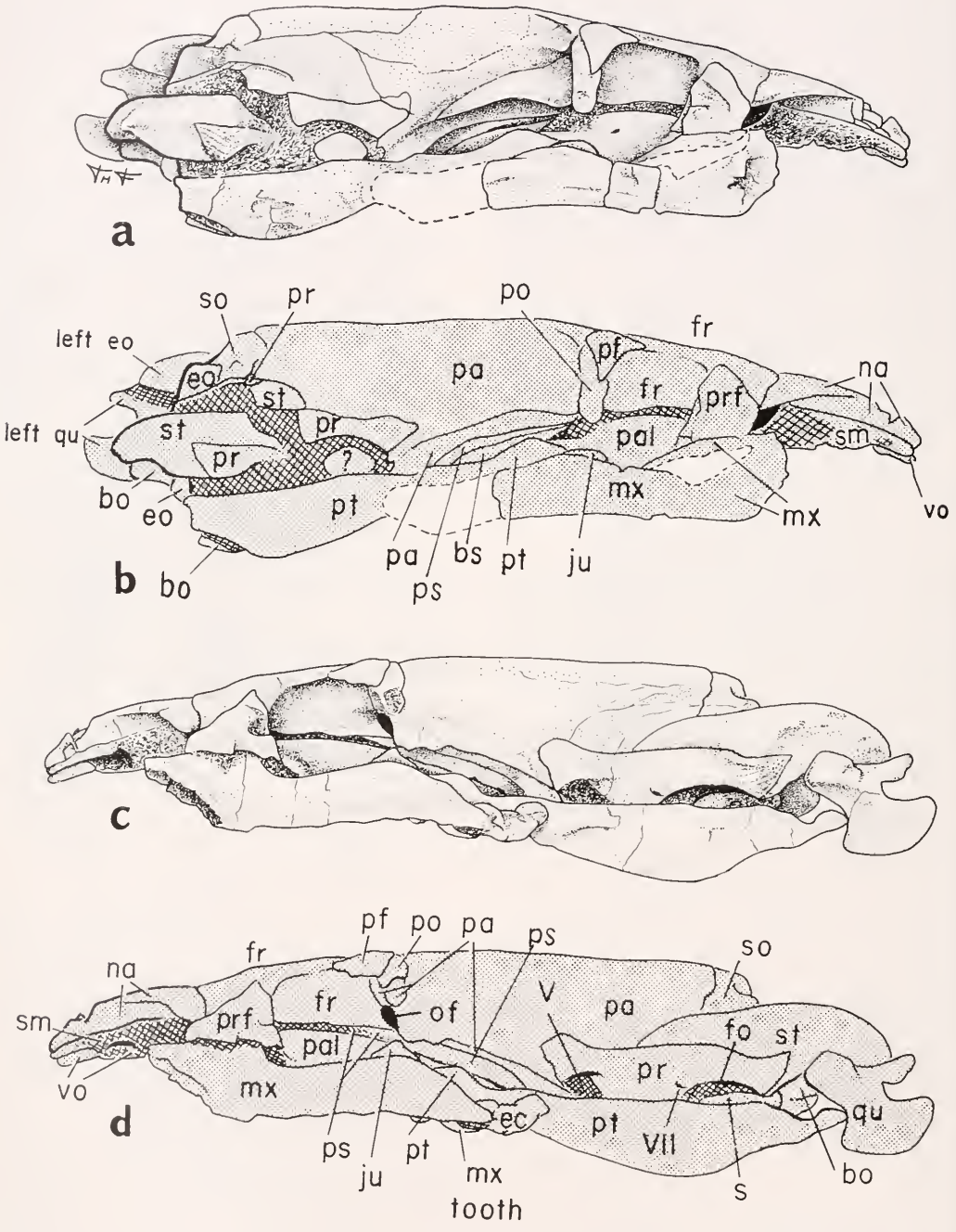


Figure 3. *Dinilysia patagonica*; lateral views of skull. Abbreviations on p. 62. × 1.5.

shelves produce the V-shaped demarcation from the nasals that is seen in ventral view. The area of contact between nasals and frontals is thus extensive, both longitudinally and transversely.

The frontals possess lateral descending walls that meet anteriorly to enclose a single, median opening for the olfactory tracts. This opening is triangular in form with the base formed by the flattened inferior surfaces of the dorsal frontal table, and with the apex lying in the midline at a point that is posterior and ventral to the base. The base itself lies about five millimeters posterior to the level of the dorsal nasofrontal line of juncture. A suture between the two descending walls of the frontal continues caudad from the ventromedian apex of the opening and is shortly hidden from view as it passes dorsal to the vomers.

In the orbital region the descending walls of the frontals slope ventromedially at roughly 45 degrees, and are gently concave. The degree of concavity slightly increases posteriorly in the region of the optic foramen. The frontal forms the anterior border of the optic foramen. The anteroventral border is provided by a small, caudally-pointed frontal process that projects beneath the foramen and does not meet the parietal; instead, the posteroventral rim of the optic foramen is formed by the basiparasphenoid, which is closely united to the frontals along the ventral midline. The dorsal and posterior walls of the foramen are formed by the parietal. The frontal meets the parietal above the foramen and bulges laterally just beneath the postfrontal.

Postfrontal

Figs. 1, 3; pf.

There are, on each side, two distinct elements in the postorbital region. The anteriormost pair of elements contact both frontal and parietal and seem to be homologous to the postfrontals of lizards. On the right side, the postfrontal bears a lateral fingerlike portion (lacking on the left) and appears to be complete.

Each postfrontal has a horizontally flattened and tapered anterior process that lies snugly in a dorsal frontal recess along the posterolateral edge of the frontal. The lateral border of the anterior process blends smoothly with that of the frontal, but caudally it expands laterally and ventrally to lie upon the corresponding postorbital bone and adjacent parietal as the fingerlike process noted above. Neither the anterior nor the lateral process extends onto the orbital surface of the frontal.

Dorsomedially, and just posterior to the frontals, each postfrontal terminates in a short, longitudinal parietal-postfrontal suture.

Postorbital

Figs. 1, 3; po.

The second pair of elements in the postorbital region lies just beneath and slightly behind the postfrontals, and appears to represent the postorbital bones of lizards. No portion of the postorbital extends along the inferior surface of the frontal or parietal. Instead, each bone lies on the postorbital process of the parietal so that the bone is wedged between the postfrontal above and the parietal below. Posteriorly the bone is exposed beneath and behind the postfrontal, the transverse caudal border of its lateral extension paralleling that of the postfrontal. At the medial end of the short postfrontal-parietal suture, the parietal sends a short bony spur laterally that overlaps the postorbital medially (see Fig. 3). There is a small but distinct fossa ventral to each postorbital, floored and terminated medially by the parietal.

On the left side the lateral projection of the postorbital is missing, while on the right the postorbital curves ventrally as it extends laterally beyond the tip of the postfrontal. The lateral postorbital process is wider and less horizontally flattened than is the postfrontal.

The free lateral end of the right postorbital has a somewhat rough and uneven texture indicating that a still more lateroventral extension of the bone has been broken away. The situation is confused by an inconsistency in Woodward's paper. His figure of the dorsal view of the skull (Fig. 1 in Plate 1) shows the left postorbital region much as it still appears in the specimen today. On the right, Woodward figures a postorbital bar that continues ventrolaterally from the fingerlike process of the postorbital bone as figured here to connect with a peculiar element (interpreted in the present paper as a jugal) lying on the surface of the maxilla. It is unfortunate that Woodward did not figure the right lateral view of the skull, for his written description seems to contradict his pictorial presentation. He surmised that the postorbitals (= postfrontals of Woodward) "partly bounded" the orbit posteriorly, but goes on to say that the postorbital "bar is broken away on both sides." Woodward's choice of the word "broken" to describe the lack of a postorbital connection to the jugal makes it unclear whether he intended to convey that the specimen was damaged after it was illustrated, or that such a connection was never present in his specimen (in which case his figure is in error). Although his figures are somewhat unclear in several respects, they appear to be quite accurately and carefully rendered, and, if the postorbital bar is shown incorrectly, it is the only major mistake we can find in Woodward's illustrations. Furthermore, it is significant that Woodward raised the issue at all, since he regarded *Dinilysia* as a relatively unmodified snake, readily comparable to *Boa constrictor.*

It is easily possible that the postorbital bar could have been damaged during Woodward's examination of the specimen. The fossil is very brittle and, even with careful handling, several areas have crumbled away and have required restoration so that the specimen as it appears at this writing does not match our own figures as well as it first did. Unfortunately the presence or absence of a postorbital connection with the presumed jugal element influences our functional interpretation (to be presented in a future paper).

Evidence provided by the cast of the specimen in the British Museum (Natural History), and mentioned above in the section on preservation, indicates that the figure is correct, and that the postorbital bar was originally complete on the right side. The cast shows bone continuous from the skull roof to the maxilla. Woodward's statement that the postorbital bar was broken thus may have referred to breakage after the cast was made. We thus conclude, on the basis of available evidence, that when the specimen first came into Woodward's hands the postorbital met the jugal.

Parietal

Figs. 1, 3; pa.

Dorsally and anteriorly, the parietal begins between the postfrontals and postorbitals at the jagged frontoparietal suture. In this region the parietal is flattened with a slight medial concavity; this essentially flat portion quickly narrows posteriorly and continues caudally as the dorsal edge of the sagittal crest. On either side of the anterior extremity of the crest, the parietal is hollowed to form a concavity that becomes shallower posteriorly and extends anterolaterally to the level of the postfrontal-parietal suture. More laterally, the parietal contour drops sharply downward onto a prominent shelflike modification of the bone. This shelf juts laterally and somewhat ventrally so that its upper surface slopes at least 30 degrees below the horizontal; the inferior surface of the shelf is smoothly concave. Anteriorly the shelf curls upward to meet the postorbital process of the parietal. Posteriorly it extends ventrally to the anterior border of the trigeminal foramen.

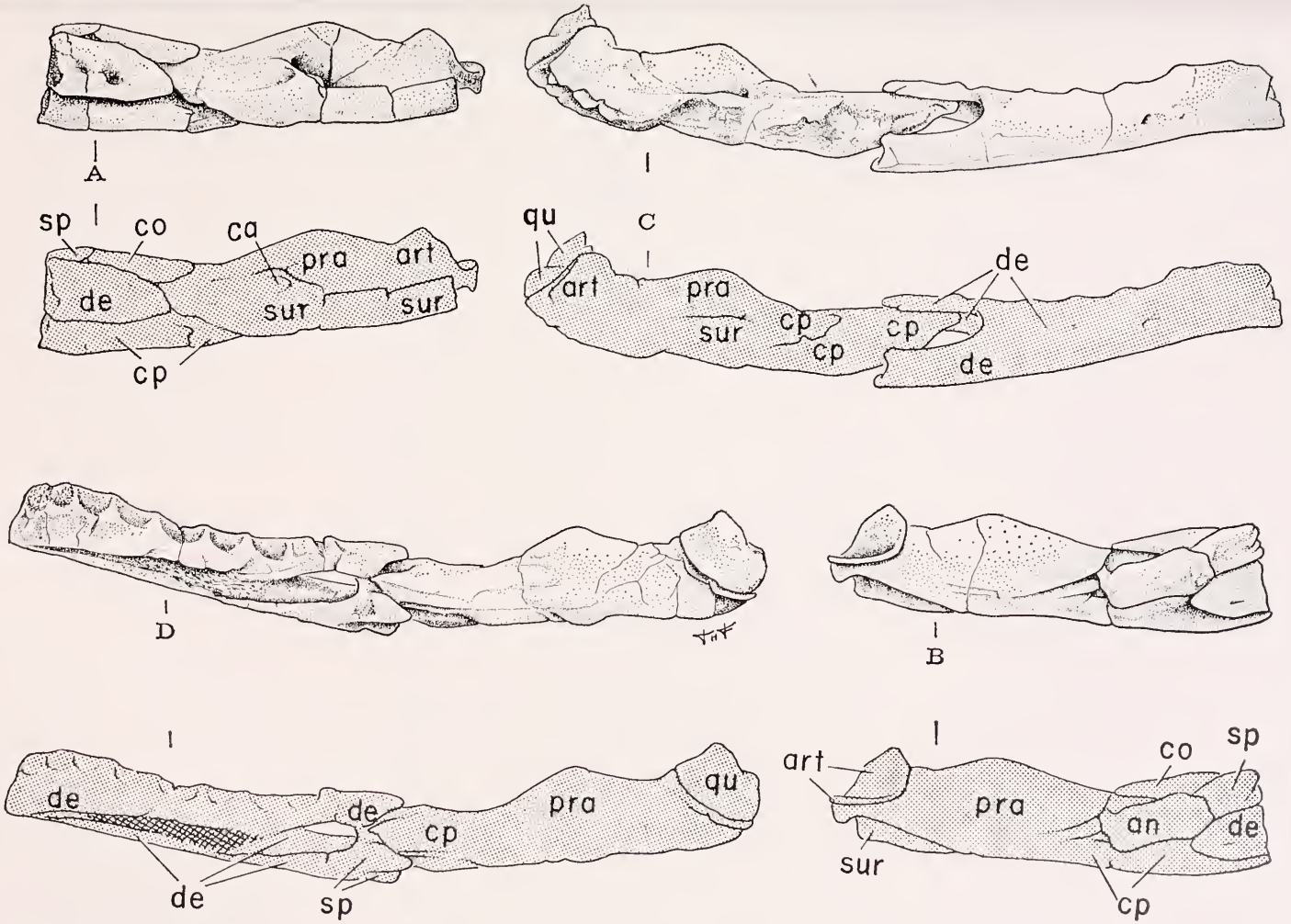


Figure 4. *Dinilysia patagonica*; A, labial, and B, lingual views of fragmentary left mandible; C, labial, and D, lingual views of right mandible in natural articulation. Abbreviations on p. 62. × 1.5.

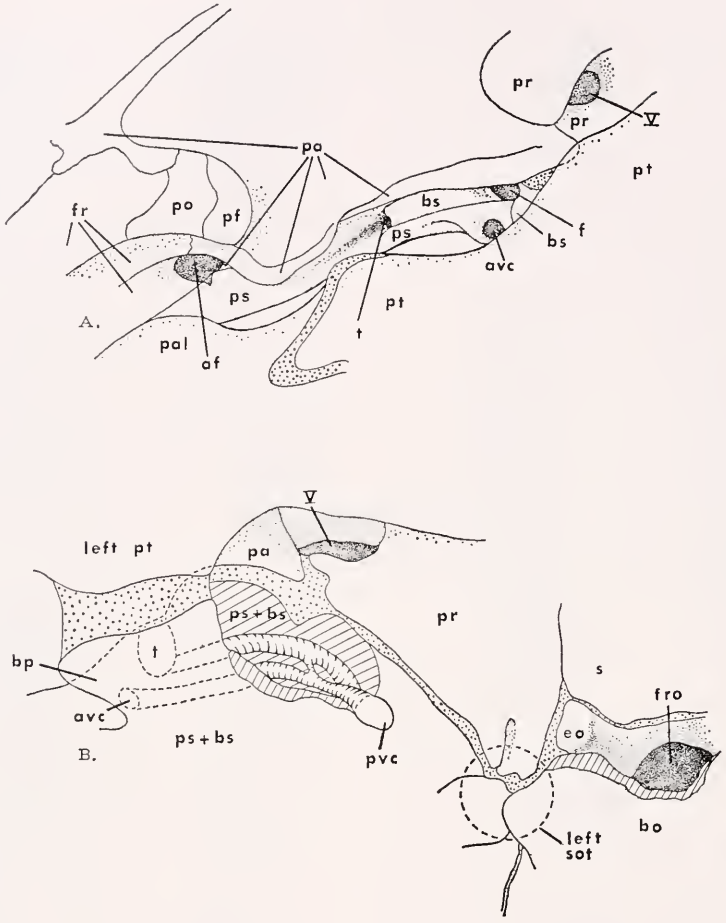


Figure 5. *Dinilysia patagonica*; A, oblique dorsolateral view of left basiparasphenoid and surrounding elements; note anterior separation of basisphenoid from parasphenoid. B, oblique ventrolateral view of area between basipterygoid process and fenestra rotunda, showing partial excavation of vidian canal and canal dorsal to it opening at f on Fig. 5a, and area between sphenopalatine tuber and stapes. Foramina in dark stipple, matrix in coarse stipple, excavated or broken areas in hatched line; abbreviations on p. 62; both × 3. Diagrammatic.

The elongated major portion of the parietal shows a faint cerebellar swelling that widens gradually until, posteriorly, it expands smoothly but markedly laterad. The parietal contacts the prootic both laterally and dorsoposteriorly, extending narrowly between the supratemporal and a dorsally exposed sliver of the prootic (see below). The parietal joins the supraoccipital posteriorly in a long, transverse suture.

Anteroventrally the parietal forms the posterior and dorsal rim of the optic foramen. In this region the ventral parietal surface joins the parasphenoid with which it is firmly sutured as far posteriorly as the anterior border of the trigeminal foramen. At the level of the basipterygoid processes of the basiparasphenoid, the parietal is developed ventrally and laterally to contribute a small, lateral portion to the base of each basipterygoid process. Immediately posterior to the level of the basipterygoid

process, the parietal is narrowly included in the anteroventral border of the single trigeminal foramen.

Prootic

Figs. 1, 2, 3, 5; pr.

The prootics are relatively large. On the left, the bone is complete, while on the right it is divided by a wide vertical fracture, which has dislocated the entire supratemporal process ventrally. Much of the ventrolateral part of the right prootic is covered by matrix and by a small piece of bone that may be a dislocated piece of the right prootic.

The anterior border of the prootic begins dorsal to the basipterygoid processes. The large, single trigeminal foramen lies in a notch on the anterior border and is almost entirely enclosed by the prootic except for a small contribution from the parietal anteroventrally. The tiny facial foramen lies on the anterior margin of the fenestra ovalis; the latter is partly excavated into the posterior border of the prootic.

Ventrally the prootic comes into broad contact anteriorly with the basiparasphenoid and extends posteroventrally to the basioccipital, contributing to the basioccipital tubera as noted below. At the level of the basiparasphenoid-basioccipital suture, the prootic is shallowly though sharply excavated to form a small, bony "step" (see Fig. 2a). This step anteriorly bounds a depression that is medially and posteriorly delimited by tuberous processes of the basisphenoid and basioccipital.

The prootic bulges laterally as it continues posteriorly onto the supratemporal process. This portion of the bone, just before reaching its caudal sutural limit with the supratemporal, is abruptly flattened in a parasagittal plane as is the adjacent supratemporal. At its posterior end, the prootic interdigitates strongly with the supratemporal and the prootic-supratemporal suture courses medially at this point on the ventral surface of the supratemporal process.

Dorsal to the supratemporal, and bounded by it, the parietal, and supra- and exoccipital elements, there is a separate, sliverlike bone, which represents an internal portion of the prootic that "breaks through" the braincase to be exposed dorsally, in isolation from the rest of the prootic. Examination of the large posterior fracture of the prootic on the right reveals that the break has cut this bony sliver, and that it is continuous with the prootic but separated externally by the long diagonal suture of supratemporal and parietal.

Supratemporal

Figs. 1–3; st.

The supratemporals begin on the transversely-expanded posterior portion of the braincase as rather narrow wedges that each lie between the parietal above and the prootic below. At the level of the dorsal prootic sliver each strip becomes vertically deepened and continues caudal to and beyond the posterior tip of the lateral part of the prootic. Here the supratemporal expands ventrally to form a parasagittally-flattened plane that is continuous with the flattened posterior surface of the prootic. Caudally, the supratemporals extend well posterior to the level of the occipital condyle and cover the lateral, and part of the ventral, portions of the enlarged paroccipital processes of the exoccipital bones.

Supraoccipital

Figs. 1, 2c–d, 3; so.

This element is a very wide, short, median bone sutured anteriorly to the parietal, laterally to the sliver-like process of the prootic, and caudally to the exoccipitals. The bone bears a median crest that is continuous with the sagittal crest of the parietal. On either side of the crest there is a ridge that begins at the parieto-supraoccipital border and extends posterolaterally to the posterior supraoccipital border, thickening progressively toward its posterolateral end. At the supraoccipital-exoccipi-

tal border, posterior and medial to the ridge, a prominent depression is present on each side.

Exoccipital and Opisthotic
Figs. 1–3; eo.

Each exoccipital (including a fused opisthotic) dorsally makes contact with the supraoccipital, prootic, and supratemporal. Posterolaterally each is expanded laterally to form a large paroccipital process that continues caudally posterior to the occipital condyle and that possesses a wide, flat superior surface facing dorsomedially. Posteromedially, the exoccipitals overhang the foramen magnum to form an awninglike rim.

Much of the occiput is formed by the exoccipitals. Here they descend to form the lateral borders of the foramen magnum and, since they join and provide the dorsal and lateral portions of the condyle, they also form most of the ventral border. Lateral to the condyle, the exoccipitals extend transversely as a pair of wide, tonguelike processes (broken off on the left) that lie beneath the paroccipital processes and floor the posterior lacerate foramina ventrally, concealing them from view. On the right, the bony tongue is well preserved, and is sutured to the basioccipital ventrally. The fenestra ovalis and the fenestra rotunda are separated by another, more ventral process of the exoccipital; this process continues ventrally and projects to meet the prootic and the basioccipital below the fenestra ovalis, where it contributes to the posterior portion of the rather complex sphenooccipital tubercle (Fig. 5b).

Basioccipital
Figs. 1–3; bo.

This unpaired ventral bone begins anteriorly at a broad, transverse suture with the basiparasphenoid. At the ends of this suture the basioccipital develops ventrally a pair of tuberous processes that lie adjacent to similar developments of the basiparasphenoid. Caudad to the level of these processes, the medial surface of the basioccipital bends dorsally, while the lateral surfaces continue posterolaterally from the tuberous processes as ventrally-developed walls enclosing a wide, short concavity. The left lateral surface is partially broken away to reveal the opening of the fenestra rotunda; on the right, the lateral wall extends toward the pterygoid.

Anterolaterally the basioccipital joins the prootics, while posterolaterally it meets the exoccipitals. Posteromedially the bone narrows and produces a transverse ridge at the base of the occipital condyle. The basioccipital forms the ventromedian part of the condyle. The basioccipital can be seen dorsally as a thin sliver separating the exoccipitals, and it contributes about one-half of the body of the condyle itself.

Basiparasphenoid
Figs. 2, 3, 5; bps.

This ventral element begins posteriorly at its transverse suture with the basioccipital, where it is bounded laterally by the prootics. The posterolateral corners are strongly developed ventrally to form a pair of tuberous processes that lie in contact with similar developments of the basioccipital. Between these processes the ventral surface of the basiparasphenoid forms a wide trough that narrows anteriorly, where it is bounded by a pair of low but sharp ventral ridges that tend to converge toward one another anteriorly. These ridges originally bore laterally-developed crests, setting off groovelike pockets dorsally. Unfortunately these delicate crests have not survived this present study, but a small portion of the right one may be seen in Figure 2a and b. Lateral to these ridges and directly posterior to the basipterygoid processes are the paired posterior openings of the vidian canals.

The laterally-placed basipterygoid processes have convex articulating surfaces that face more laterally than ventrally; their axes are anteroposteriorly elongated, and

their ventromedial surfaces are gently concave. The ventral margin of each process is thickened and is separated slightly from the pterygoids. The joint between the processes and the pterygoids is straight and has a slight anteromedial-posterolateral orientation. The dorsal sides of the processes are partially covered by moderate ventral downgrowths of the parietals. The anterior vidian canals occur far laterally on the basipterygoid processes.

The parasphenoid and basisphenoid are separate anterior to a foramen that opens dorsomedial to the anterior opening of the vidian canal (Fig. 5). The lateral and medial borders of this foramen are formed by the basisphenoid, its visible dorsal border formed by the parietal, and its ventral border by the parasphenoid. The basisphenoid extends anteriorly from this foramen about one-third of the distance to the optic foramen. At this point on both sides it stops abruptly at prominent, matrix-filled trabecular grooves (Fig. 5a), and the parasphenoid expands dorsally to meet the parietal, filling the gap in front of the basisphenoid. The trabecular grooves lie wholly in the cultriform process of the parasphenoid, although they approach the parietals closely.

The cultriform process of the parasphenoid is wide posteriorly near the basipterygoid processess, but tapers anteriorly and is closely pressed to parietal, basisphenoid, and, presumably, frontals. The inferior surface of the bone, between the basipterygoid processes and its meeting with the palatines, bears a distinct, elongated concavity.

The tapered anterior end of the parasphenoid extends between and slightly dorsal to the palatines; the tip stops short of the posterior extremities of the vomers.

STAPES

Figs. 2, 3; s.

On the left side, posteroventral to the prootic, there is a stapes consisting of a relatively large footplate and, as preserved, a delicate columellar process. Medially the bone is inserted into a fenestra ovalis, which is in turn set into a deep cleft in the posterior surface of the deeply emarginated prootic and the exoccipital. The fenestra ovalis is separated from the fenestra rotunda by an anteroventrally-projecting process of the exoccipital. The columellar process is broken, but extends toward the quadrate and approaches the posterior portion of the pterygoid. Whether or not it abutted against the quadrate is conjectural because of columellar breakage and quadrate dislocation.

SUSPENSORIA OF THE PALATO-MAXILLARY ARCH; THE ARCH ITSELF

Prefrontal

Figs. 1–3; prf.

The prefrontals are horizontally flattened so that their entire lateral surfaces could be equally well designated as dorsal. Since the prefrontal forms the anterior orbital wall, this flattening extends the orbit laterally so that it opens as much superiorly as laterally.

The external surface of each prefrontal (better preserved on the left than on the right) is roughly an equilateral triangle, with the lateral side lying upon a dorsal expansion of the maxilla, and the medial corner forming a dorsal tonguelike process that is inserted into the upper frontal surface. The anterior prefrontal margin extends from this dorsal corner and crosses the lateral corner of the nasal to terminate against the maxilla.

The ventral tonguelike process that lies against the lower frontal surface bears a pronounced transverse elevation that caudally delimits a deep prefrontal concavity that opens medioanteriorly. The ventral edge of this elevation is expanded anteriorly as a flattened, horizontal surface that comes into contact with the palatine and maxilla.

Posteriorly, in the anterior orbital region,

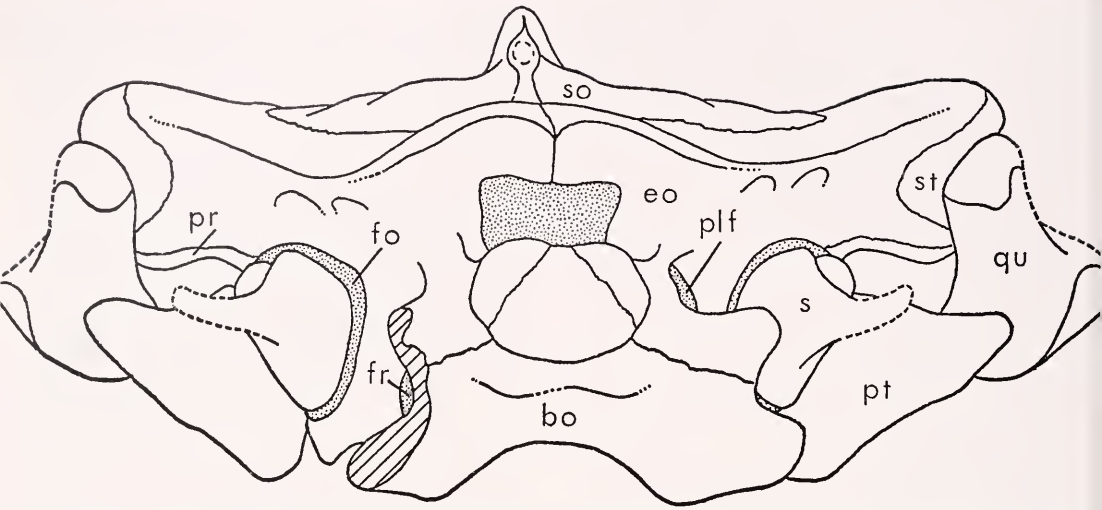


Figure 6. *Dinilysia patagonica*; reconstruction of occiput. Abbreviations on p. 62. × 3.5. Dotted line = conjectural; structures missing on one side restored from the other; broken exoccipital-basioccipital hatched and not restored, in order to show fenestra rotunda. Diagrammatic.

each prefrontal descends and then flattens horizontally where it rests upon the upper surface of the lateral palatine process (see below). Here the prefrontal is perforated by the combined orbitonasal canal and lacrimal foramen, which on both sides is nearly closed ventrally by the prefrontal.

Palatine

Figs. 2a–b, 6; pal.

The palatines lack toothed anterior projections. Instead, the dentigerous portion does not extend anteriorly beyond the level of the lateral process of each palatine. A distinct, deeply impressed choanal channel is present, which is partially closed ventrally by sheetlike expansions from both lateral and medial edges of the palatine. Medial to the choanal channel, the sheetlike expansion is pressed against the lateral and inferior surfaces of the vomer as described above. The posterolateral dentigerous portion of each palatine is a thick, ribbonlike process facing ventromedially, and is rather smoothly continuous with the medial process. No teeth are preserved but small sockets for the subpleurodont teeth are perceptible. If we may judge by the diameters of their sockets, the palatine teeth were relatively small. They extended forward in a single row from the palatopterygoid joint to the posterior level of the lateral palatine process. It is impossible to determine precisely their number; we estimate that each palatine bore about five or six teeth.

The lateral process of the palatine is formed by a sudden horizontal expansion and flattening of the lateral palatine edge, just anterior to the level of the first palatine tooth. This expansion provides a partial floor beneath the choanal passage in that region, but its major portion stretches laterally over the superior surface of the medial maxillary process and beneath the prefrontal. The lateral palatine process is very extensive in that it intervenes between prefrontal and maxilla in such a way as to all but prevent those elements from coming into contact, and it reaches transversely nearly to the ventrolateral edge of the prefrontal. Below the lacrimal foramen, the lateral palatine process is perforated by a transversely-widened maxillo-palatine foramen.

In dorsolateral view, just in advance of the dorsal lappet of the pterygoid, a tiny (venous?) foramen pierces the dorsal surface of the longitudinal portion of the palatine (Figs. 3, 8c).

Posteriorly the palatines join the pterygoids in a rather complex manner. Dorsolaterally the pterygoid sends forward a pointed projection that seems to lie in a correspondingly shaped shallow depression in the palatine surface. Ventrally (partially preserved on the left side) similar pointed processes are mostly broken away but presumably extended onto the undersurface of the palatine, as indicated by depressions in the bones. In effect, the palatine was clasped by these two projections (cf. Figs. 5a, 8c, 10a).

Pterygoid

Figs. 1–3, 5–6; pt.

The anterior attachments of the pterygoids with the palatines have just been described. The pterygoid tooth row is continuous with that of the palatine. It appears, upon examination of the tooth sockets, that the approximately five pterygoid teeth were subequal to those on the palatine and that they diminished in size posteriorly. The last tooth socket lies just ahead of the level of the basipterygoid joint.

The internal process of the pterygoid is moderately developed, arises at the level of the basipterygoid, and meets the ventrolaterally facing basipterygoid surface.

At the level of the internal process, the lateral side of each pterygoid joins with an ectopterygoid. Again at the same transverse level, but dorsally, each pterygoid bears a sharp longitudinal ridge. Slightly posterior to this point the pterygoid becomes sharply compressed, the upper edge of the ridge continuing caudally as the dorsal margin of the compressed pterygoid portion. The posterior, compressed portion of the pterygoid is convex laterally and concave medially. Posteriorly the vertical dimension increases to the level of the basicranial tubera and then decreases posteriorly; the dorsal border remains longitudinally straight. In ventral view, the posterior halves of the pterygoids are essentially straight. The posterior tips of the pterygoids (as seen on the left) are applied to the medial surface of the quadrate.

A small, pebblelike element (labelled "?" in the figures) lies upon the dorsal surface of the right pterygoid. This is probably a dislodged fragment of the nearby broken area of the prootic as noted above.

Maxilla

Figs. 1, 2a–b, 3, 7; mx.

Woodward's figure shows the right maxilla as complete (Fig. 1 in Plate 1). It is sad to note that today neither maxilla is complete anteriorly. It is also regrettable that Woodward figured only the dorsal view of the right maxilla. On the original cast (Plate 2) the maxilla curves conspicuously downward anteriorly, is strongly excavated for the naris, and reaches almost to the midline.

At the present time, the maxilla on the left is somewhat better preserved than that on the right. In the region of the prefrontal, the lateral maxillary surface is flattened and turns upward to meet the lower margin of that element. The lateral maxillary surface is smooth and convex anteriorly; posteriorly it is somewhat dorsoventrally expanded and concave.

Dorsally, the superior maxillary surface receives the lateral palatine process that intervenes between prefrontal and maxilla. This process is very loosely articulated with the maxilla and is separated from it by a deep, matrix-filled groove. In this region the maxilla sends forth a flattened medial process that is seen in ventral view to extend mediad along the ventral surface of the palatine.

More posteriorly the maxilla bears a marked ridge running lengthwise on the dorsal aspect of the bone. This ridge sharply

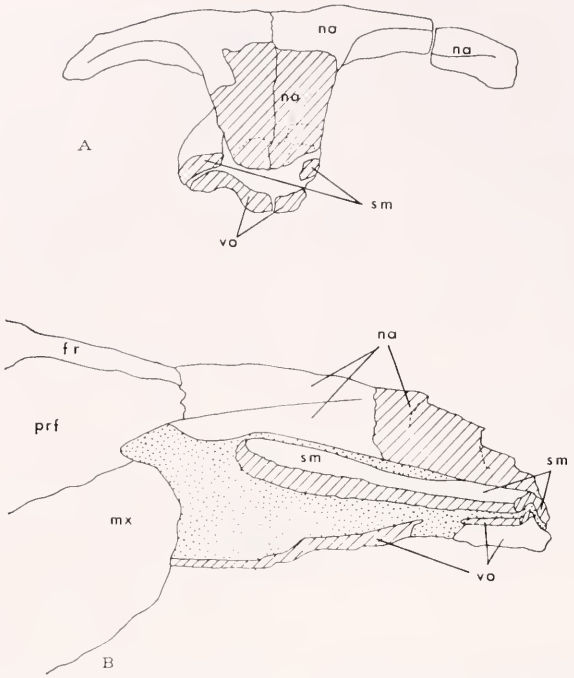


Figure 7. *Dinilysia patagonica*; A, anterior, and B, right lateral view of snout region; hatched line = broken surfaces. Abbreviations on p. 62. × 3. Diagrammatic.

separates the lateral maxillary surface just described from the medial side of the maxilla. The surface of the medial side faces dorsomedially; caudally it becomes increasingly concave to form a rather deep, longitudinal channel that extends to the posterior limit of the bone. Lying in this channel, on each side, is a small fragmentary element interpreted here as the jugal (see below).

Ventrally each maxilla has a row of tooth sockets that follows the ventrolateral edge of the bone. Much of the ventral area is obscured on the right; on the left, there is evidence of seven maxillary teeth on the specimen today, but the cast indicates that at least thirteen maxillary teeth were originally present. There is no clear indication that the teeth decrease markedly in size posteriorly.

The posterior two sockets on the left contain remains of teeth. The anterior tooth is very fragmentary. The caudal surface of the more posterior tooth is hidden by matrix, and its tip is broken away. However, its anterior and ventral surfaces are intact and visible; it arises from the maxilla as a thick, basal portion from which it curves very markedly caudad to give the appearance of a sharply bent cone. The backward sweep of this tooth does not quite lie in a parasagittal plane, but slants slightly inward at an angle of approximately 20 degrees to the longitudinal axis.

Posteriorly the maxillae are joined by the ectopterygoids (mostly absent on the right). Here the left maxilla bears, along its medial margin, a longitudinal groove (for the ectopterygoid) that extends forward to the level of the middle of the jugal.

Ectopterygoid

Figs. 1, 2a–b, 3c–d; ec.

Unfortunately neither ectopterygoid is well preserved, and the right element is al-

most entirely lacking (though it was nearly complete in 1901). On the left, the ectopterygoid arises from the lateral edge of the pterygoid and, in the form of a small cylinder, passes forward and outward to the maxilla. It appears to abut against the caudal maxillary tip and to cover a very small portion of the upper maxillary surface, and a groove on the medial surface of the maxilla indicates that it once extended anteriorly to the level of the middle of the jugal.

Jugal

Figs. 1, 2a–b, 3; ju.

A small bone lies in the longitudinal channel formed on each side of the dorsomedial maxillary surface. These elements are essentially symmetrical in position and in shape and are unlikely to be adhering fragments broken from some other portion of the skull. Each of these peculiar bones has the form of a flattened ellipsoid whose anterior end is turned upward toward the tip of the postorbital. They appear not to be portions of the ectopterygoids that have been accidentally isolated, since grooves for the anterior extensions of the latter occur on the medial sides of the maxillae. These bones are best interpreted as jugals.

In the natural condition, the dorsally turned anterior portion of the jugals must have made contact with the postorbitals as indicated on the original cast (see above, Postorbital).

Quadrate

Figs. 1–3; qu.

Much of the left quadrate remains and is still attached to the skull. Its lateral surface is peculiarly flat, suggesting that a portion of this surface has been sheared off. The lower portion of the right quadrate is articulated with the right mandible; there is no remaining trace of the upper portion.

The quadrate was apparently a somewhat triradiate structure. The posterior arm of the left element extends caudally behind the enlarged paroccipital process and the anterior portion is deflected laterally, indicating that the bone has slipped posteriorly. The normal position of the quadrate must have been more anterior, and the anterior quadrate arm must have come close to the caudally flattened part of the prootic.

The ventral arm of the essentially triradiate quadrate is somewhat flattened anteroposteriorly and expanded transversely. Its lower end curls posteriorly, presenting a smoothly convex hemispherical articulation surface ventrally.

The lateral side of the posterior end of the pterygoid articulates with the medial quadrate surface just dorsal to the level of the hemispherical expansion. The articulation surface was originally further anterior on the pterygoid before distortion of the quadrate.

MANDIBLES

Fig. 4

Three mandibular fragments have been preserved. These consist of the posterior half of the left mandible, whose broken anterior end is neatly severed, and a nearly complete right dentary and a right "compound bone." The right elements can be fitted together, as shown in the figures, although they were originally distorted as shown in the original cast (Pl. 2) and in Woodward's figure (Pl. 1). The left dentary, present at the time of Woodward's study, has been lost.

Compound Bone

Fig. 4; cp.

Different portions of the two compound bones possess badly eroded surfaces and parts. Examined together, however, the two bones provide a rather complete interpretation of the natural condition.

The articular area forms a shallow cup that opens dorsomedially to receive the hemispherical lower end of the quadrate

in a ball-and-socket joint. No retroarticular process of any sort is present, although the ventral surface of the mandible is broken posteriorly, and this region cannot be reconstructed with certainty.

The surangular process is represented only by a low, smooth, longitudinal ridge on the lateral surface of the compound bone. The prearticular ridge is well developed with a bluntly pointed dorsal contour. Between the surangular and prearticular processes the small mandibular fossa opens. Immediately anterior to this, the surangular bears a shallow longitudinal channel in its dorsal surface that extends alongside a narrower, rather inconspicuous channel on the anterolateral border of the prearticular lamella. The two channels together form an elongated concave area for coronoid articulation.

The right compound bone has lost the elements (coronoid, angular, splenial) that naturally adhere to it, and its anterior structure can be studied. The anterior end bears a short medial, and a larger lateral, projection. At the point where the two projections begin to diverge, a shallow groove runs posteriorly in which lay the coronoid. The ventral surface of the larger projection itself bears a groove (for the upper posterior end of the dentary) that ends abruptly near the base of the projection.

When articulated with the dentary, the larger lateral surangular projection fits in a notch between the dorsal and ventral caudal ends of the dentary; the shorter, medial projection makes contact with the splenial bar that connects the medial edges of the dorsal and ventral dentary ends.

Dentary

Fig. 4; de.

Only the right dentary is preserved, although fragments of the posterior end of the left still remain attached to the posterior bones. The dentary curves mediad anteriorly, is slightly pointed and seems not to have been firmly united with its fellow on the left.

Posteriorly the dentary forks into dorsal and ventral processes that are free laterally but are connected medially by the splenial. By comparison with the left mandible, the dorsal, tooth-bearing process on the right is seen to be incomplete at its lateral border, but the ventral process has only minor posterior breakage. The lateral notch between them communicates with Meckel's groove on the medial side. The lower, medial surface of the splenial bears a spleniodentary suture. A large, elongated alveolar foramen is formed between the splenial and the ventral surface of the tooth-bearing border of the dentary.

Anteriorly, on the medial side, Meckel's groove becomes narrower and approaches the ventral dentary margin where it terminates shortly behind the dentary tip.

Ten large tooth sockets are borne by the dentary as preserved, and also on the original cast of the left dentary. In addition to these, at least one smaller tooth socket may be present close to the anterior tip of the bone, but this is uncertain because of breakage. The size of the teeth appears to have diminished slightly caudad.

Splenial

Figs. 4c–h; sp.

A portion of the splenial is preserved on the left in articulation with the posterior bones, and its articulation with the dentary is shown on the right.

On the left, a somewhat rectangular piece of bone is identifiable as the splenial by its position. It is bordered dorsally by the coronoid and upper dentary process, posteriorly by the angular, and ventrally by the lower dentary process.

Coronoid

Figs. 4e–h; co.

The right coronoid is missing. A portion of the left coronoid lies in a shallow groove

medial to the dorsal tooth-bearing process of the dentary. Anteriorly it lies between the dentary on the dorsolateral side, and the splenial on the medial side. Posteriorly this fragment stops short of the prearticular lamella.

The coronoid must have extended posteriorly into the groove on the dorsal surface of the compound bone noted above; the latter bears striated attachment surfaces for its reception. The coronoid must have forked posteriorly, one part ascending the prearticular ridge medially as indicated by a roughened articulation surface, the other forming a coronoid process of unknown extent laterally on the surangular; the two processes thus complete the relatively narrow mandibular fossa anteriorly.

Angular

Figs. 4g–h; an.

An angular appears only on the left mandible. It is short and thick as preserved, but can be seen to have extended posteriorly to the level of the mandibular fossa. It is traversed by a high ridge that extends the length of the preserved portion of the bone and probably did so throughout its original length, since a ridge is still present at the posterior end of the suture area.

The angular is positioned somewhat ventromedially and is slightly slanted upward anteriorly. Its anterolateral corner approaches, but no longer reaches, the coronoid; a groove presently exists between breakage surfaces of the two bones and it can only be surmised that the two bones met. The angular also makes extensive contact with the splenial anteriorly and touches the posterolateral edge of the lower caudal dentary process.

Foramina of the Skull

Foramina are described briefly under the sections dealing with bones in which they occur; for convenience, a description of skull foramina in the context of their surrounding bones is given here. Terminology follows that of Bahl (1937), although we do not necessarily agree to the appropriateness of the names applied.

The tiny lacrimal foramen (lf, Figs. 1, 8c) is completed dorsally by prefrontal and ventrally by palatine. Medially it seems to be confluent with the relatively large orbitonasal canal (oc, Figs. 1, 8c); the latter is floored ventrolaterally by the palatine.

The maxillo-palatine foramen (mp, Figs. 1, 8c) lies wholly within the lateral (maxillary) process of the palatine bone.

Dorsally, the anterior border of the optic fenestra (of, Figs. 3c–d, 5) is formed by the frontal, while posteriorly it is surrounded by the parietal. Its ventral border is completed by the parasphenoid.

Both anterior and posterior openings of the vidian canal (pvc, Figs. 2a–b, avc, Fig. 5) perforate the basipterygoid process of the basiparasphenoid. Both openings are about the same size. Mechanical excavation of the basipterygoid process shows that the vidian canal has a tiny, short anastomosis dorsally with a canal that appears to come from within the cranial cavity and leads anteriorly to an opening dorsal to the anterior opening of the vidian canal (Fig. 5). The dorsal canal is formed dorsally by the parietal, laterally by the basisphenoid, and ventrally by the parasphenoid. After leaving the anterior opening, the contents of the canal have left a channel on the basisphenoid.

The trigeminal foramen is single, and relatively large (V, Figs. 3c–d, 11a). It lies almost wholly within the prootic, but anteroventrally it receives a small contribution from the parietal.

The facial foramen (VII, Figs. 2c–d, 3c–d, 11a) opens through the prootic at the anterior margin of the fenestra ovalis.

The fenestra ovalis (Figs. 2c–d, 12a) is quite large, but it cannot be seen directly because of the massive, superimposed stapedial footplate. The foramen is formed by deep emarginations in the posterior part

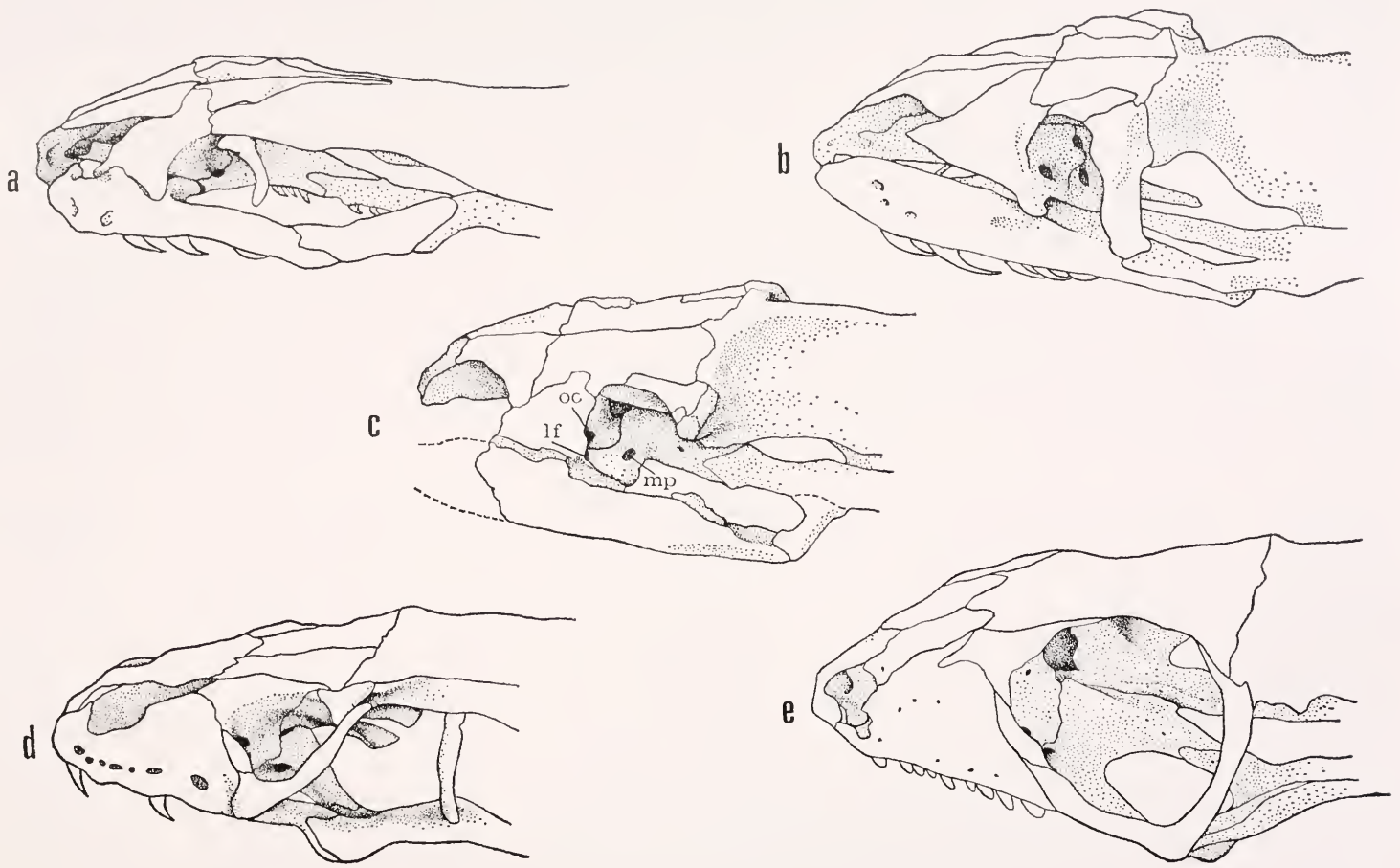


Figure 8. Oblique dorsolateral view of a, *Cylindrophis maculatus*, MCZ 34885, × 4.5; b, *Python molurus*, MCZ 4278, × 1.5; c, *Dinilysia patagonica*, × 1.5; d, *Lanthanotus borneensis*, MCZ 8305, × 4.5; e, *Tupinambis nigropunctatus*, MCZ 109890, × about 2.5. Abbreviations on p. 62. Semidiagrammatic.

of the prootic and the anterior border of the exoccipital. The latter sends a lappet ventrally to the spheno-occipital tubercle; presumably this lappet represents a fused opisthotic.

The fenestra rotunda (fro, Figs. 2c–d, 12a) is large. Dorsally it is separated from the fenestra ovalis by the lappet of exoccipital described above, and ventrally it is completed by the basioccipital.

The foramen lacerum posterius (plf, Figs. 2c–d, 12a) opens through the posterior surface of the exoccipital, lateral to the foramen magnum. In occipital view, it is concealed behind a small tongue of the exoccipital. No separate hypoglossal foramina are associated with it on the occipital surface, nor does excavation show that such foramina appear within the mouth of the foramen.

The foramen magnum (Figs. 2d, 12a) is surrounded by the exoccipitals, except ventrally, where the latter are separated on the midline by a tiny wedge of basioccipital.

Comparisons dealing with the foramina appear within the context of the discussion below.

DISCUSSION

Comparisons of *Dinilysia* with modern snakes indicate that it shows greatest similarity to the primitive snake families Boidae and Aniliidae (*sensu lato*), especially to the latter. However, the aniliid complex is itself in great need of study: no detailed osteological descriptions of *Loxocemus*, *Xenopeltis*, *Cylindrophis*, or *Anilius* exist. In addition, *Dinilysia* has some characters that appear unique and others that invite comparison with lizards rather than with snakes. A full scale comparison of *Dinilysia* with all the forms that should be utilized will be a lengthy task and one requiring an abundance of illustration. It is, in fact, still in the future.

We feel, however, the need to put *Dinilysia* in its approximate context at this time. Without making every comparison or providing final judgment on its position in the phylogenetic sequence, we do wish to call attention to its most conspicuous characters indicate its position relative to other snakes and most obvious resemblances, and so and to lizards, as we now see it.

To do this as nearly as possible without bias, we have chosen as the specimens to be used for our first comparisons with *Dinilysia* a few primitive snakes, *Python sebae* and *Epicrates cenchris* (described by Frazzetta, 1959), and certain lizards, *Lanthanotus borneensis* (discussed by McDowell and Bogert, 1954), *Varanus monitor* (elaborately described by Bahl, 1937), *Tupinambis nigropunctatus* (taken as an example by Jollie, 1960), *Mabuya carinata* (described by Rao and Ramaswami, 1952) and *Ctenosaura pectinata* (discussed by Oelrich, 1956). We have added a few observations from skulls of *Cylindrophis* and *Anilius* at hand. By these admittedly very specific, but we hope judiciously distributed comparisons, we have tried to avoid the unjustified generality of statement that afflicts so many discussions of the characters and relationships of higher groups. We admit out of hand that comparisons so secured will not necessarily be the most relevant. However, until thoroughgoing investigation provides greater assurance, we can present only a very preliminary assessment of the position of *Dinilysia*. We do not pretend to attempt more. *When, therefore, in the comparison below we contrast lizards and snakes, we mean no more than that within our sample all the lizards and all the snakes were each congruent with the other examined members of their suborder.*

We shall score below (in italicized phrases) the ascertainable characters of *Dinilysia* as "snakelike," "lizardlike," "intermediate" or "unique." Here again the statements should be taken only in the context of the comparisons expressly made. Certain comparisons are omitted at this time, e.g.

comparisons with the as yet poorly understood typhlopids and leptotyphlopids.[1]

The skull of *Dinilysia* is incomplete, but its preserved parts will be discussed *seriatim*, following the sequence of the description.

No indication of premaxillae exists at present; however, the original cast of the specimen (Plate 2) shows the right maxilla extending close to the midline, appearing to imply that the premaxilla was originally of relatively small lateral extent. The smooth tip of the maxilla on the cast probably indicates a loose articulation with the premaxilla, as in extant snakes, instead of the sutural connection characteristic of lizards. *This feature therefore would be scored as a strong resemblance to snakes.*

The descending lamellae of the two nasals in *Dinilysia* are extremely thick and short and together form an extraordinarily robust septum almost one-third as wide as the widest part of the two horizontal nasal lamellae above (Fig. 7). In snakes there are thinner, deep, sharply defined descending nasal lamellae (Frazzetta, 1959). In lizards there is instead a cartilaginous nasal septum. *In having a bony rather than a cartilaginous nasal septum* Dinilysia *is snakelike. In the thickness of its septum it is unique.*

The vomers of *Dinilysia* are visible between the palatines ventrally as a pair of slender, rodlike processes with limited vertical or lateral extent (Figs. 2, 10), rather than the prominent vertical lamellae of the vomers in extant Boidae (Frazzetta, 1959: 457). In lizards the vomers may have considerable lateral expansion (e.g. *Lanthanotus* but not *Varanus*). *In neither snakes nor lizards are the vomers underlain by a portion of the palatines (see below) as they appear to be in* Dinilysia. *The vomers of* Dinilysia *are thus neither snakelike nor specifically lizardlike.*

In *Dinilysia* the frontals have lateral descending walls that meet to enclose a single median anterior opening. In boid snakes the frontals form *a pair* of openings by sending down not only lateral but median walls to surround the olfactory tracts. Lateral walls descend from the frontals in *Varanus* and *Lanthanotus* but not in *Ctenosaura*, *Tupinambis* or *Mabuya*. *The presence of lateral descending walls of the frontal in* Dinilysia *represents a step toward the snake condition and one that would be expected in an intermediate form.*

The nasofrontal articulation is extensive in *Dinilysia* and the frontals send elongated lappets anteriorly under the nasals. The overall extensiveness of the contact contrasts with the type of articulation between frontal and snout complex described in snakes (Frazzetta, 1959, 1966). Evidently snout mobility about the nasofrontal joint was less than, or at least differed from, that of boids. Discussion of the type of kinesis possible in *Dinilysia*, and the comparison of this with lizard and snake kinesis is, however, deferred to a future paper (Frazzetta, in preparation). *The difference from snakes in the extent or kind of mobility between nasals and frontals, and the relationship of nasals and frontals is lizardlike and primitive.* This difference is surprising only if it is accepted that one of the primary and defining adaptations of snakes is a prokinetic joint that permits rotational movements (see Albright and Nelson, 1959; Frazzetta, 1966).

The anteriormost element in the postorbital region is probably homologous to the postfrontal of lizards; the posterior probably is the postorbital. There has been some uncertainty regarding homology of the saurian postfrontals and postorbitals

[1] We have deliberately not included comparisons with the Scolecophidia (Typhlopidae and Leptotyphlopidae). We have felt (1) that the most evident resemblances were as much lizardlike (or primitive) as scolecophidianlike, (2) that the striking differences were specializations of the Scolecophidia irrelevant to the phyletic position of *Dinilysia*, and (3) that the Scolecophidia, like the Aniliidae, still need much careful study before much worthwhile can be said about them, although we have included statements about the latter group because of its clear relationship to *Dinilysia*.

with the ophidian elements in this region. The relationships of the two bones present in this region of *Dinilysia* have the same relationships to the frontal, parietal, and jugal as do the postfrontal and postorbital of *Tupinambis*. Neither bone extends medially along the descending frontal wall or contacts the prefrontal as does the pythonine supraorbital (Frazzetta, 1959: 461). We have thus no hesitation in homologizing these elements with the comparable ones of lizards. The supraorbital of pythons may be of heterotopic origin; a specimen of *Python molurus* examined by Frazzetta (FMNH 100419) has several such bones in the supraorbital area. On the other hand, it is equally possible that the pythonine supraorbital is the postfrontal of lizards, as suggested by McDowell and Bogert (1954). The presence in *Dinilysia* of twin bones having the saurian relationships to other skull bones gives the virtue of parsimony to the latter interpretation. For reasons noted in the description, we believe that a complete postorbital bar was present in *Dinilysia*, with the postorbital joining the jugal. A postorbital arch is present in boids but is joined to the palatomaxillary arch only by a ligament; the *Dinilysia* condition differs importantly in retention of the jugal —although a very peculiar jugal (see below). *The retention of both postfrontal and postorbital is a primitive squamate feature and might plausibly be expected in any very primitive snake.*

Dorsally the parietals of *Dinilysia* are applied to the occipital and otic bones, as in snakes; there is thus no posttemporal foramen like that of lizards. *In this feature* Dinilysia *is snakelike.*

The parietals in *Dinilysia* descend to provide a complete lateral covering to the brain, as in snakes. In none of the compared lizards is there any trace of a similar enclosure of the brain by the parietals. (In lizards there is also an epipterygoid in this region, which is absent in snakes and of which there is no evidence in *Dinilysia*.) *The parietal downgrowths in* Dinilysia *are unequivocally snake characters.*

In *Dinilysia* the descending lamina of each parietal forms the anterior border of the trigeminal foramen as the similar lamina does for the anterior trigeminal foramen in *Epicrates*, *Anilius* and *Cylindrophis*, but not in *Python*. In the compared lizards, lack of the descending parietal lamina results in the trigeminal nerve taking its exit from a notch in the prootic rather than from a foramen. *The* Dinilysia *condition is again a snake character.*

The prootic is large in *Dinilysia*, larger than in the compared boids and lizards. In sharp contrast with the boids, there is only one trigeminal foramen bounded anteriorly by the parietal and hence anteriorly placed in a position, as before mentioned, comparable to the *incisura prooticum* of lizards and the anterior trigeminal foramen of *Epicrates*, *Anilius*, and *Cylindrophis*. *In this feature* Dinilysia *is lizardlike and more primitive than boid snakes but this feature is plausible in a very primitive snake.*

In *Dinilysia* the prootic is broadly notched posteriorly for the relatively enormous stapedial footplate, larger relatively than the very large footplates of *Anilius* and *Cylindrophis*. *Unlike these bones in snakes, the otic and occipital bones do not surround the footplate with a pericapsular chamber and the whole of the footplate is thus exposed as in lizards.* The exposed stapedial footplate is primitive and lizardlike, and, while not found in boids or advanced snakes, again might plausibly be expected to occur in a very primitive snake. The proportions of the stapes, with its large footplate and small, posterodorsally-directed columellar process, are as in *Anilius* and *Cylindrophis*, although even in the latter two forms the footplate is not relatively so large. The relative size of the stapes is unexpected and may be special to *Dinilysia*. *The stapes of* Dinilysia *has a generally lizardlike aspect, but in exposure of footplate, proportions of footplate to*

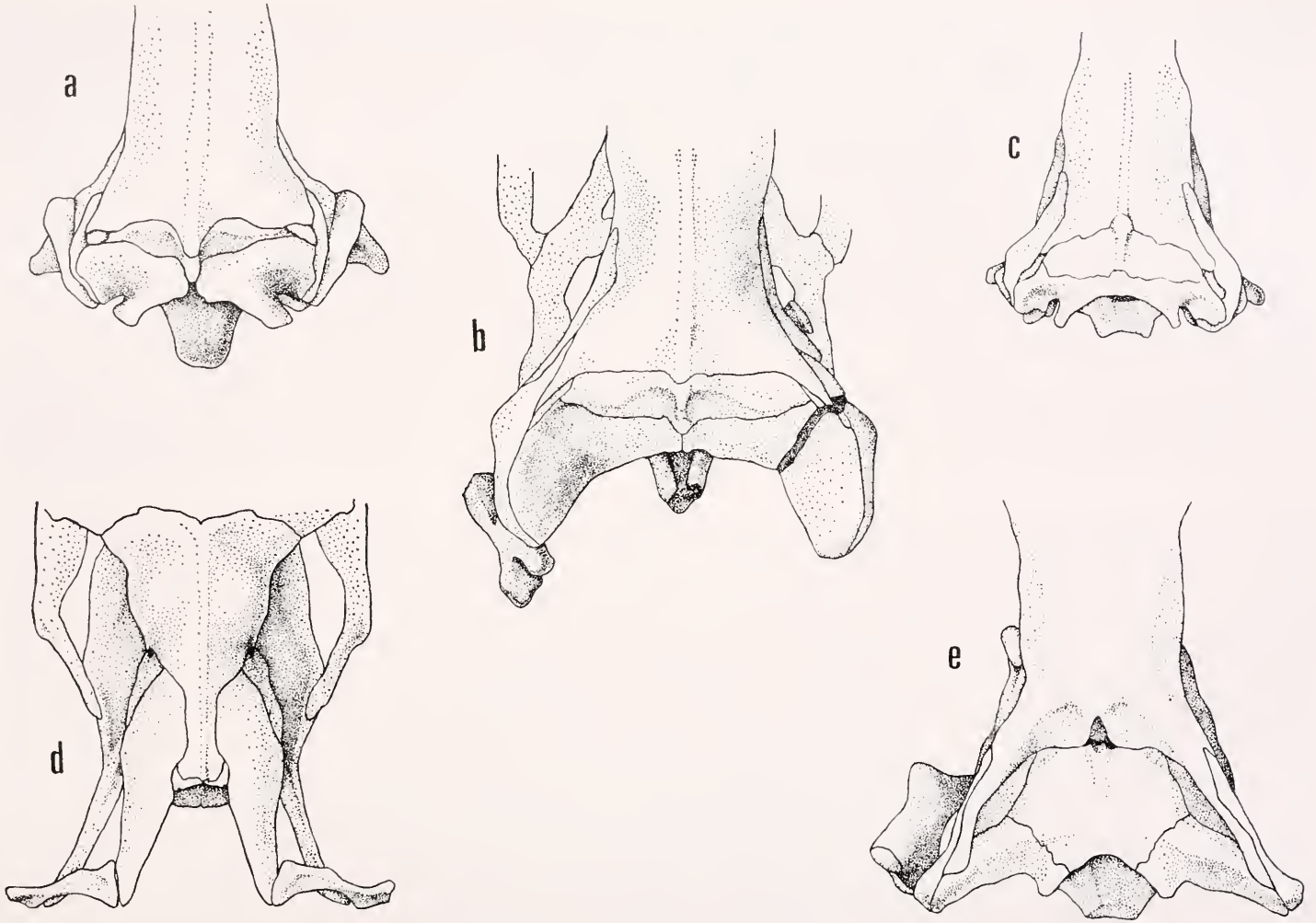


Figure 9. Dorsal view of posterior skull region of a, *Cylindraphis moculatus*, MCZ 34885, × 4.5; b, *Dinilysia patagonica*, × 1.5; c, *Anilius scytale*, MCZ 857, × 4.5; d, *Python molurus*, MCZ 4278, × 1.5; e, *Lanthonotus borneensis*, MCZ 8305, × 4.5. Right quadrates missing in b and e. Abbreviations on p. 62. Semidiagrammatic.

columellar process, and connection of the latter to the footplate by a strong posterior crest (Fig. 6, etc.), it is specifically Anilius*-like.*

The presence of a small dorsal exposure of the prootic, and its relation to surrounding bones, is exactly like the situation in *Anilius* and *Cylindrophis* (Fig. 9).

The massive supratemporals of *Dinilysia* are completely applied laterally to the paroccipital processes of the exoccipitals. They are like those of *Anilius* or *Cylindrophis* in being incorporated into the skull. They differ strikingly from the supratemporals of *Anilius* or *Cylindrophis* and resemble those of boids in being drawn out lateroposteriorly to a level *well behind* that of the occipital condyle, but are unlike those of boids in lacking a long *free* posterior projection: the paroccipital processes of *Dinilysia* are applied to the supratemporals all the way to their distal ends (Fig. 9).

The supratemporals of lizards are also very different: small, almost vestigial in *Ctenosaura* and *Mabuya*; relatively large in *Lanthanotus* and *Tupinambis*. In the latter two, however, most of the slender supratemporal lies alongside the posttemporal wing of the parietal; only a smaller posterior portion overlies the paroccipital process to make contact with the quadrate. In all compared lizards, posterior termination of the supratemporal lies only slightly behind the posterior level of the occipital condyle.

The supratemporal of Dinilysia *combines lizard and snake (in fact, boid) features in an unexpected way.* The strong association of supratemporal and paroccipital process is lacertilian, as we have stated, but the way in which the supratemporal is carried well behind the occipital condyle is like the situation in boids and suggests a way in which the slender exposed supratemporal of boids may have evolved: to obtain the snake condition from that characteristic of eosuchians and lizards we need only to have supratemporal and paroccipital process extend well posteriorly with a posttemporal foramen present; next, as in *Dinilysia*, to close the foramen by secondary growth of supraoccipital and opisthotic; and then to achieve the more usual snake condition by secondarily reducing the paroccipital process to the anterior level from which it began. The incorporation of such an intermediate stage would not be obvious were it not in front of us. Interpretation of the sequence of functional adaptations that may have been involved in such an evolutionary series will necessarily require analysis of the mechanics of the entire skull and, if this evolutionary sequence is verified as occurring in the main line of snake origins, will have great importance for our understanding of the way of life of the first snakes.

The supraoccipital in *Dinilysia*, in its shape and relationships to surrounding bones, is closely comparable to this element in *Cylindrophis* and *Anilius* and is relatively much lower than the wedge-shaped element of *Python* or the vertical blade of *Epicrates*. In *Dinilysia*, as in the boids, *Anilius*, and *Cylindrophis*, a median knob on the supraoccipital continues the strong sagittal crest on the parietal. In contrast, lizards have either a median crest on the supraoccipital (*Ctenosaura*, *Tupinambis*; "processus ascendens" of Oelrich, 1956) rising to meet the parietal, the whole surface of which is at a distinctly higher level than that of the body of the supraoccipital, *or* (*Lanthanotus*, *Mabuya*) parietal and supraoccipital are at the same level at the point of contact but a small unossified prong ("processus ascendens tecti synotici" of most authors; "cartilaginous portion of the processus anterior" of Rao and Ramaswami, 1952) fits into a notch of the parietal. The difference in appearance of the two conditions in lizards *inter se* and as compared with conditions in *Dinilysia* and snakes is considerable. *In this regard,* Dinilysia *is clearly snake-like and specifically* Cylindrophis-Anilius*-like.*

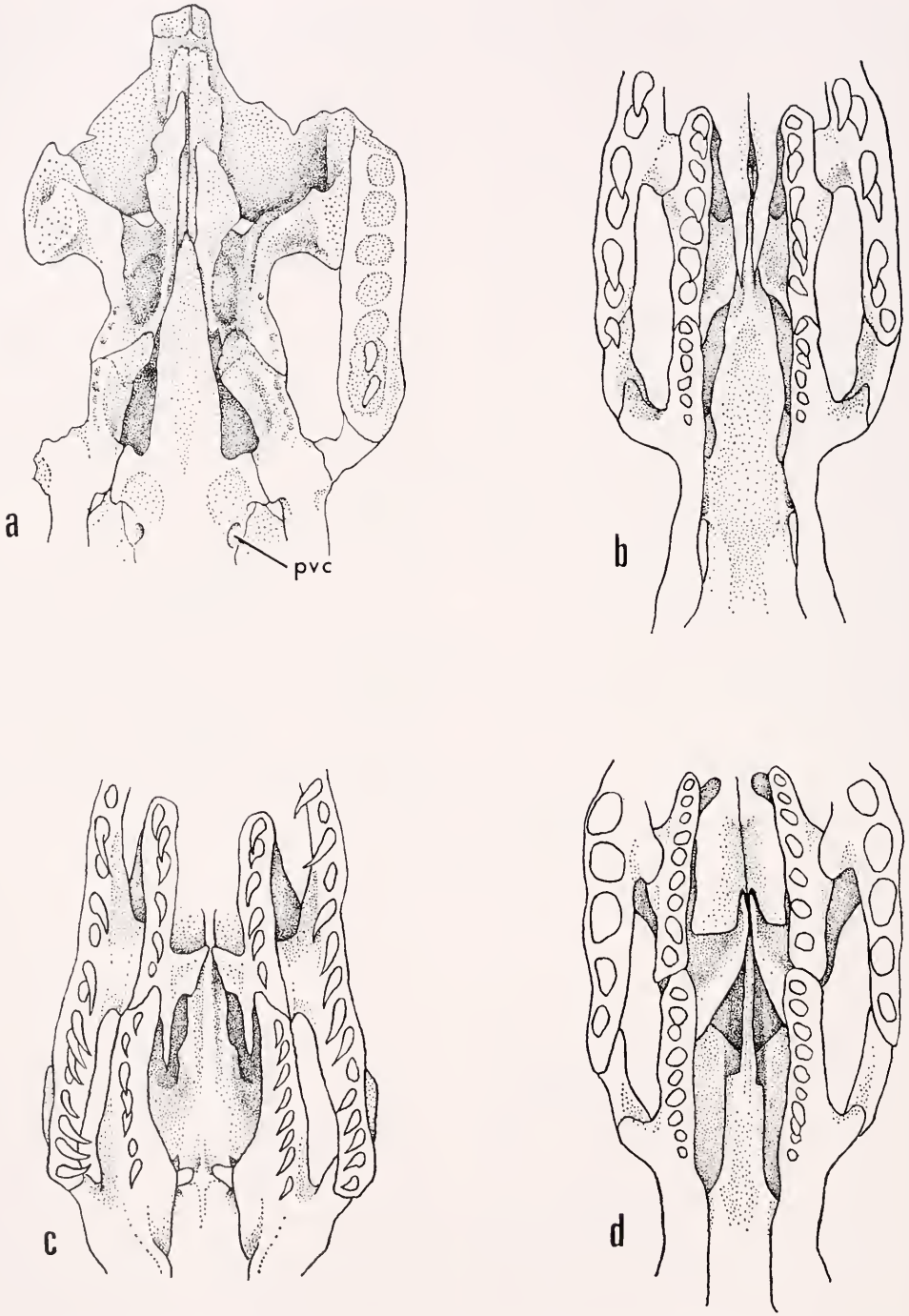


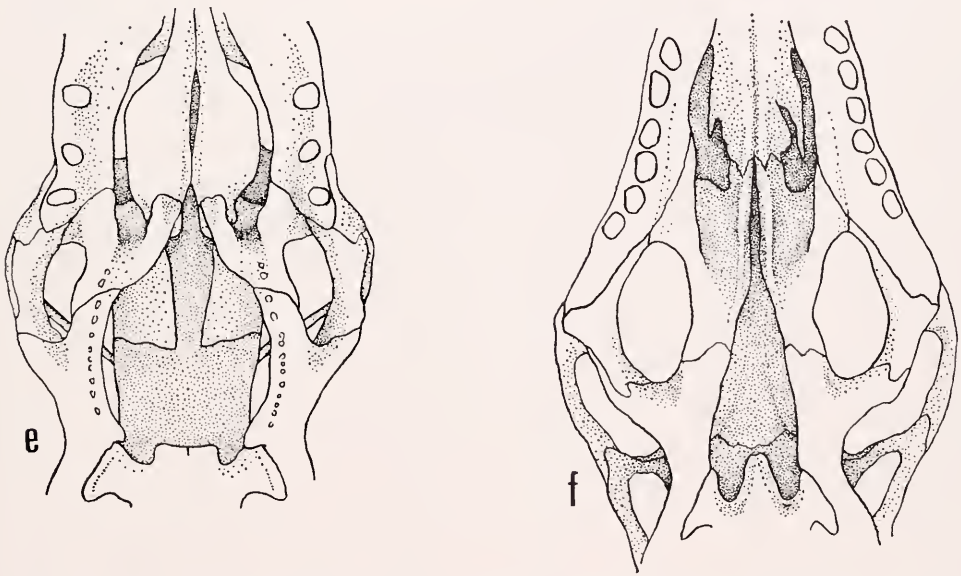
Figure 10. Palatal region of a, *Dinilysia patagonica*, × 1.5, right maxilla and ectopterygoid removed; b, *Cylindraphis maculatus*, MCZ 34885, × 4.5; c, *Python malurus*, MCZ 4278, × 1.5; d, *Anilius scytale*, MCZ 17645, × 4.5; e, *Lanthonotus borne-*

The exoccipitals of Dinilysia *are in one regard strikingly snakelike: they meet on the midline and exclude the supraoccipital from the edge of the foramen magnum.* The flat broad shelf that the exoccipitals form above the occipital condyle is, however, continued smoothly into the strong paroccipital process, which is carried backward with the supratemporal behind the occipital condyle, as noted above. This is in contrast to the condition in boids, in which the median exoccipital shelf ends abruptly in a notch separating the shelf from a rudimentary paroccipital process that at its extreme lateral projection does not extend further posteriorly than the extreme posterior level of the shelf and the condyle below it (*Python*), *or* does not extend further posteriorly than the level of the lateral margins of the foramen magnum (*Epicrates*).

In lizards the exoccipitals are always well lateral. They do not exclude the supraoccipital from the foramen magnum and may provide a very rudimentary lateral shelf over the foramen magnum (*Ctenosaura*, *Mabuya*, *Lanthanotus*) or none at all (*Tupinambis*). In lizards the paroccipital process is more robust than in snakes but in no case does it project strongly backward carrying the supratemporal with it behind the level of the occipital condyle, as in *Dinilysia*.

As in both lizards and snakes, each exoccipital in *Dinilysia* forms a lateral third of the occipital condyle. As in *Python* and *Epicrates*, a lappet of exoccipital extends posteriorly underneath the moderate-sized posterior lacerate foramen, which faces directly posteriorly. In *Anilius* and *Cylindrophis* the posterior lacerate foramen faces more laterally than posteriorly and the bony process underneath is likewise posterolateral. Of the lizards compared, only *Lanthanotus* has a ledge beneath the posterior lacerate foramen and this forms a shallow trough leading posterolaterally (Fig. 12).

The exoccipital in *Dinilysia* participates in the dorsal margin of a large, widely-open fenestra rotunda that is directed ventro-



ensis, MCZ 8305, × 4.5; f, *Tupinambis nigropunctatus*, MCZ 109890, × about 2.5. Abbreviations on p. 62. Semidiagrammatic.

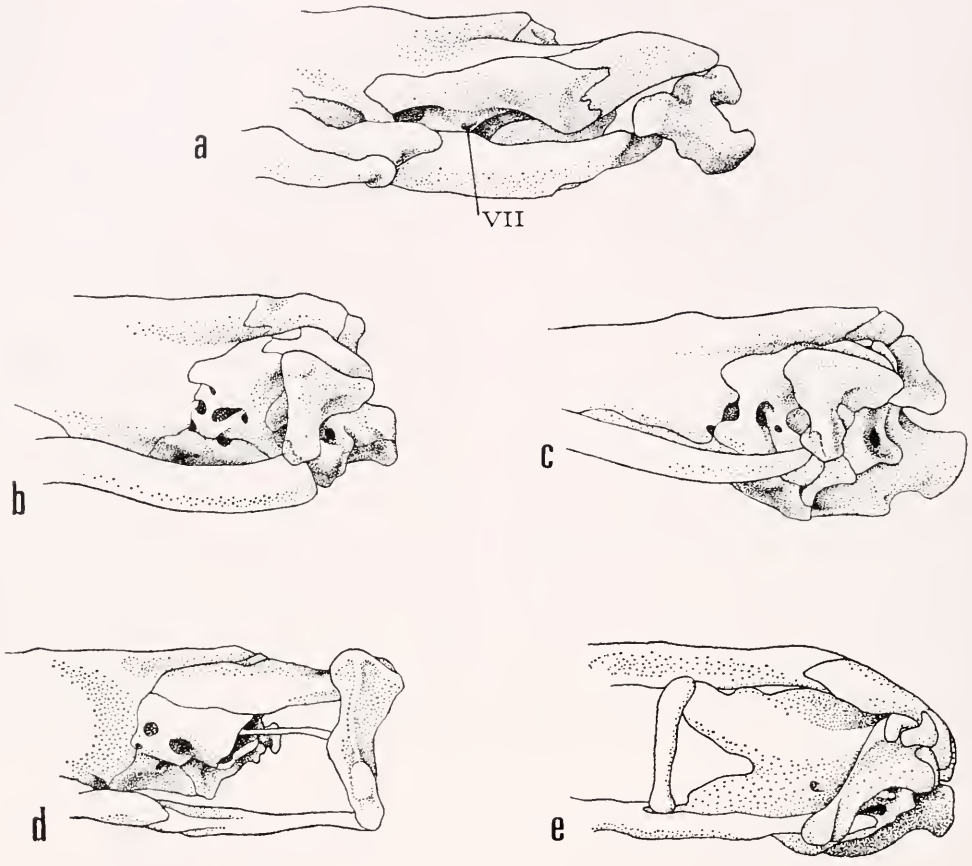


Figure 11. Lateral view of posterior skull region of a, *Dinilysia patagonica*, × 1.5; b, *Anilius scytale*, MCZ 17645, × 4.5; c, *Cylindrophis maculatus*, MCZ 34885, × 4.5; d, *Python molurus*, MCZ 4278, × 1.5; e, *Lanthanotus borneensis*, MCZ 8305, × 4.5. Abbreviations on p. 62. Semidiagrammatic.

laterally. In snakes (*cf.* Baird, 1960), the fenestra ovalis (partly) and fenestra rotunda (wholly) are enclosed and almost walled off from view by a *crista circumfenestralis*, except in *Anilius* and *Cylindrophis*, in which the crista is not prominent and the stapedial footplate relatively large.

The crista circumfenestralis of snakes appears to correspond to the crista tuberalis of lizards (Säve-Soderbergh, 1947: 512; see also Oelrich, 1956: 1–17). The latter crista begins at the root of the paroccipital process and extends ventrally to the sphenooccipital tubercle (Oelrich), forming a posterior wall for the fenestra rotunda. The snake condition can be derived from that of lizards by the growth forward and upward of the crista tuberalis until the fenestra rotunda is deeply concealed at the base of the crista, which then partly occludes the fenestra ovalis and encloses the stapedial footplate. The crista tuberalis in *Dinilysia* does not fully enclose the stapedial footplate and the fenestra rotunda is thus widely open as in *Anilius*, *Cylindrophis*, and lizards, but the fenestra rotunda is strikingly low on the occiput (below, instead of on the level of the condyle), a condition not found in the lizards and *a fortiori* not in snakes (Fig. 12).

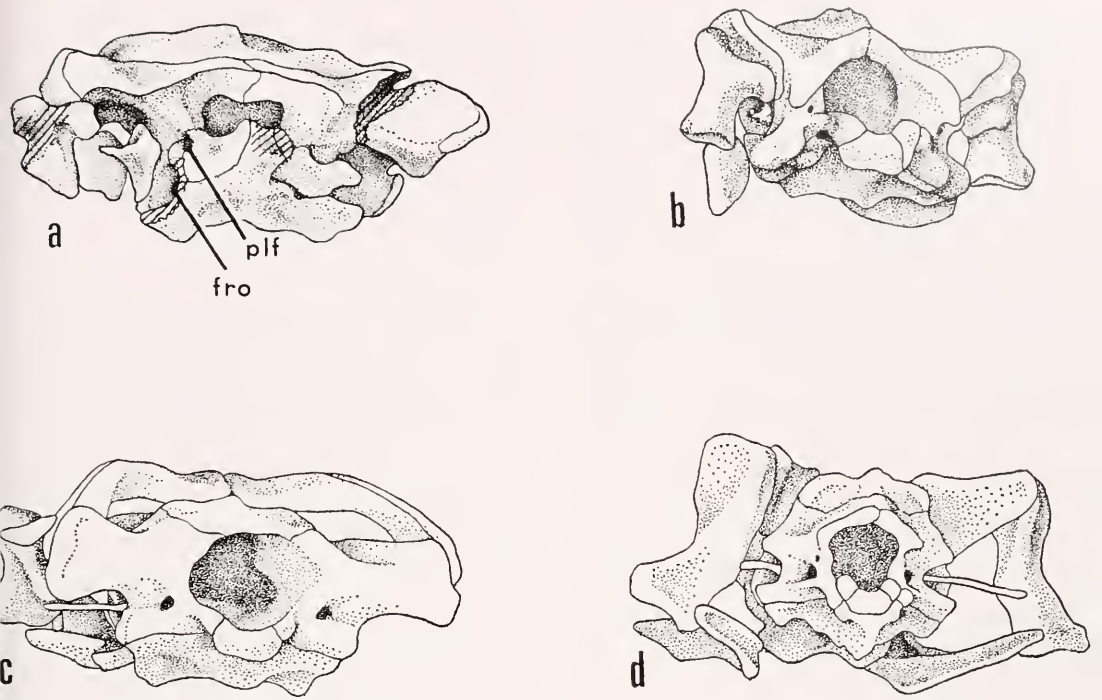


Figure 12. Oblique posterior view of occiput of a, *Dinilysia patagonica*, × 1.5, hatched lines = breakage; b, *Anilius scytale*, MCZ 17645, × 4.5; c, *Lanthanatus borneensis*, MCZ 8305, × 4.5; d, *Python molurus*, MCZ 4278, × 1.5. Right quadrates missing in a and c. Abbreviations on p. 62. Semidiagrammatic.

The absence of a crista circumfenestralis in Dinilysia *is presumably a primitive condition and thus again is very plausible in a primitive snake. The low position of the fenestra rotunda, on the other hand, is clearly associated with the relatively enormous size of the stapedial footplate and may, like the latter, be special to* Dinilysia.

The basioccipital in *Dinilysia*, as is usual in lizards and snakes, provides a median third of the occipital condyle. *As in lizards, there are large, projecting spheno-occipital tubera forming between them a concave channel on the ventral surface of the basioccipital.* The very large extent to which the basioccipital participates in the posterior as well as ventral wall of the fenestra rotunda is unusual. In snakes the crista circumfenestralis, which is wholly of exoccipital origin, widely separates the basioccipital from the fenestra rotunda. In *Lanthanotus* the basioccipital forms only a small part of the lower edge of the fenestra, and this narrow participation seems the usual lizard condition. *The extensive participation of the basioccipital in the wall of the fenestra rotunda in* Dinilysia *is closer to the lizard than the snake condition.*

The laterally-placed basipterygoid processes of the basiparasphenoid have convex articulating surfaces that face more laterally than ventrally, and the axis of the processes is anteroposteriorly elongated. This situation is in contrast to the closely spaced, ventrally-facing, lateromedially-elongated structures seen in boids, and more closely resembles the lizard configuration. On the other hand, the processes in lizards have a narrower stem and an expanded distal articulation in contrast to the broad, even width of the processes in *Dinilysia*. In *Anilius* and *Cylindrophis* the basipterygoid articulations

are lateral and anteroposteriorly elongated, as in *Dinilysia*, but the articulations in these two snakes are scarcely raised from the body of the basiparasphenoid. *Here the resemblances are partly to lizards and partly to the* Anilius-Cylindrophis *complex.*

The wide bladelike cultriform process of *Dinilysia*, gently concave ventrally, bears a striking resemblance to that of *Cylindrophis.* Even *Anilius* has a narrower, if stout, cultriform process, while those of lizards are feeble and thin as well as narrow, frequently distorted and curved upward in the dry skull. *The strength of the cultriform process in* Dinilysia *is snakelike but the specific resemblance is, as stated, to that of* Cylindrophis (Fig. 10).

The prefrontals in *Dinilysia* have a wide, firm, interlocking contact with both frontals and maxillae, much as in *Anilius* and *Cylindrophis.* In contrast *Epicrates* and *Python* have only a loose contact between prefrontals and maxillae. In lizards there are, of course, firm sutures with both bones but the prefrontal has little lateral exposure, being covered by the ascending process of the maxillae. In *Dinilysia*, as in *Lanthanotus*, *Varanus* and snakes, the prefrontals intervene between the maxillae and nasals. *The resemblance again is snakelike but specifically to* Cylindrophis *and* Anilius *rather than boids* (Fig. 8).

The palatines of *Dinilysia* are strikingly unsnakelike in the absence of anterior toothed projections. In this respect they are like the palatines of lizards. Like lizards they have strong, wide medial processes to the vomers. Unlike *Lanthanotus*, *Varanus*, or *Ctenosaura* but like *Tupinambis*, these medial processes are deeply excavated for the choanal passages. Rather similar medial processes of the palatines occur in *Anilius* and *Cylindrophis*, but, as in *Tupinambis*, these processes at their medial terminations lie between or dorsal to the posterior ends of the vomers; they do not broadly underlie them as in *Dinilysia* (Fig. 10). *Here* Dinilysia *resembles some lizards and seems more primitive than boids, but shows both some special resemblances to* Cylindrophis *and* Anilius *and some unique features as well.*

The dorsal surface of the palatine encloses the posterior opening of the maxillopalatine foramen in *Dinilysia*, as in *Python*, *Lanthanotus*, *Cylindrophis*, and *Varanus* but not as in *Mabuya*, *Tupinambis* or *Anilius.* In *Ctenosaura*, according to Oelrich, this foramen may be wholly within the palatine or may be completed laterally by the maxilla or the jugal or both. *This character appears to have little value for the placement of* Dinilysia *or any other form* (Fig. 8).

The tooth row on the posterior prong of the palatine of *Dinilysia* is gently curved and is continued by a row likewise gently curved on the pterygoid. This is unlike the straight rows (and much larger teeth) of snakes. The curvature is like that of *Lanthanotus*, but the pterygoid teeth are very much smaller in the latter. Other lizards are even more dissimilar. It is important that on the pterygoid and palatine in *Dinilysia* teeth appear to be enlarging and approaching the snake condition, but clearly in both size and in the curvature of the row they are some steps behind the snake condition. The implication would appear to be, as with the absence of the *anterior* toothed prong of the palatine, that in *Dinilysia* the characteristic method of snake feeding was not yet perfected.

The posterior quadrate process of the pterygoid of *Dinilysia* is a vertical plate with a sharp ventral edge as in lizards and *Cylindrophis*, not as in boids and *Anilius*, which have the ventral edge rotated medially so that the process is no longer a vertical plate. *It is interesting here that there is a resemblance to* Cylindrophis *as well as to lizards.*

The maxilla of *Dinilysia* is snakelike in its long, gently tapering anterior end and slight ascending process meeting the prefrontal; its general shape is specifically like

that of *Cylindrophis*. The two teeth that are preserved are comparable to those of snakes in their sigmoid conical form and in their implantation. *The snake resemblance is clear, and within snakes the resemblance is to* Cylindrophis.

The ectopterygoid in *Dinilysia* is a short and simple bone joining the lateral process of the pterygoid and the maxilla. If any slender process extended along the medial surface of the maxilla to provide much of the dorsolateral rim of the suborbital fenestra, as in boids, especially *Python*, it has not been preserved. There may have been a short anteromedial process, as in *Cylindrophis* and *Anilius*. In *Tupinambis* such a process excludes the maxilla from the margin of the suborbital fenestra. In *Varanus* and *Lanthanotus* the maxilla is similarly excluded from the suborbital fenestra, but this seems to be a result of the shortening of the maxilla (see McDowell and Bogert, 1954) rather than of any long anterior prong of the ectopterygoid. In other lizards a short anteromedial process is present: this is presumably a primitive character. *The* Dinilysia *ectopterygoid seems unspecialized and, if taxonomically important, is so only in its differences from certain forms, not in its resemblances.*

The element we interpret as a jugal is absent in snakes and is quite unlike any lizard jugal in form and position. Its rounded shape, and its occurrence in a trough on the dorsal surface of the maxilla, are unique. In lizards the jugal is characteristically larger and has more extensive contacts, not only with the maxilla as in *Dinilysia*, but with the ectopterygoid (all examined cases) and with the postfrontal or postorbital and sometimes (*Ctenosaura, Mabuya*) the squamosal. According to Jollie (1960), reduction or loss of the jugal accompanies loss of orbital and temporal arches as in burrowing forms or geckos. In snakes, both arches are gone but, if our interpretation of *Dinilysia* (as influenced by the original British Museum cast) is correct, the jugal did in this form make contact with the postorbital and completed the orbital arch. It is thus peculiar, primarily in its shortened and compact form, lack of contact with the ectopterygoid, and insertion in a groove of the maxilla. The presence of a jugal in *Dinilysia* is a primitive character and is thus expected in a very primitive snake. Its special features are, however, wholly surprising and require special functional study. At the moment, it would seem more probable that these special conditions are peculiar to a specialized side branch and are not part of the main line transition in the shift from lizard to snake adaptive zones.

The extensive attachment of quadrate to paroccipital process is unlike that of any boid. *Anilius* and *Cylindrophis* approach *Dinilysia* in degree of expansion of the head of the quadrate, and in the short and dorsoventrally-compressed shape of the bone. The strongly curved tympanic process of the quadrate is unlike that of any other squamate, but is approached in *Anilius* and *Cylindrophis*. *The oval distal quadrate articulation of* Dinilysia *is a unique feature and does not resemble the irregular articulation surface of lizards, or the related, more saddle-shaped snake condition* (see below, articular, and Frazzetta, 1959, figs. 1, 2). Again functional considerations and interpretations are important, but there now seems to be no reason to postulate the transformation of the lizard joint into the *Dinilysia* condition, and then to return to the saddle-shaped joint of snakes as part of the lizard–snake transition; this condition seems again to emphasize that *Dinilysia* is a specialized side branch of the early booid radiation.

The dentary is like that of snakes in having a strong reentrant notch posteriorly for the surangular. *No specific resemblances to lizards occur, and the general aspect is more as in boids than as in* Anilius *or* Cylindrophis. *In this feature* Dinilysia *resembles the snakes.*

The splenial is small and meets the angular in a vertical suture. *The resemblance here is to snakes, although the vertical splenial-angular suture occurs also in* Lanthanotus.

The angular, in its shape, position, and articulation with the splenial is like that of snakes.

The compound bone is complex and its resemblances less clear-cut than those of the dentary. It resembles that of snakes in having a narrow surangular projection fitting loosely into the dentary notch, and in lacking (apparently) a retroarticular process. It is unique in having a small mandibular fossa that is dorsal and dorsolateral in orientation, cut off from medial exposure by a strong ridge on the prearticular area, and exposed laterally by the absence of such a ridge on the surangular region. The prearticular ridge occurs in snakes, but it is relatively larger in *Dinilysia* and more acutely angled. The lack of a strong surangular ridge for the coronoid differs from the condition in any snake or lizard. *In* Dinilysia, *while the relations with the dentary and the apparent absence of a retroarticular process constitute a general approach to snake conditions, the mandibular fossa and articular joint form one of the most peculiar and unique features of this animal.*

The coronoid is in great part missing, but it has left articulation surfaces on the compound bone that allow some interpretation of its extent. In its relationship to the mandibular fossa, it shares some of the unique features of the latter. Two distinct articular surfaces occur at the anterior end of the fossa, one on the medial (prearticular) ridge, the other a deep notch immediately lateral to the fossa. This suggests that the coronoid forked narrowly around the anterior border of the fossa. *While the forking is a lizard feature, the close apposition of the two parts of the fork is unique to* Dinilysia. The main body of the coronoid projected vertically, forming a coronoid process of unknown extent, and then culminated anteriorly in a strong, flat ventromedial strap of bone that is all that remains today of the coronoid bone itself. *This preserved part of the coronoid is as in snakes and lizards generally, except in* Anilius, *in which the coronoid is almost vestigial.*

SUMMARY

Dinilysia is conspicuously a mosiac of primitive and specialized characters. It has lizardlike features and also some startling and unique peculiarities, but it is also clearly a snake and it has some detailed resemblances to the modern primitive snakes *Anilius* and *Cylindrophis* that seem difficult to dismiss as convergent.

The snakelike features—in fact booid snakelike—are as follows: (1) absence of temporal arches; (2) probable loose connection of premaxilla and maxilla; (3) presence of a bony nasal septum; (4) ventral enclosure of the brain by both frontal and parietal downgrowths; (5) absence of a posttemporal foramen; (6) parietals level with oto-occipital complex; (7) descending process of parietal completing trigeminal foramen anteriorly; (8) supraoccipital participation in sagittal crest; (9) exoccipitals excluding supraoccipital from foramen magnum; (10) lappet of bone present behind posterior lacerate foramen; (11) prefrontals intervening between maxillae and nasals; (12) reduced ascending process of maxilla; (13) strong, movable reentrant articulation of dentary and surangular on lateral side of mandible.

Characters more specifically similar to the *Anilius-Cylindrophis* complex are: (1) relatively large size of stapes, especially the footplate; (2) the peculiar dorsal exposure of the prootic; (3) wide-bladed *Cylindrophis*-like cultriform process of the parasphenoid; (4) prefrontal having a firm union with maxilla and frontals; (5) posterior (quadrate) process of pterygoid a vertical plate as in *Cylindrophis*; (6) quad-

rate a dorsoventrally compressed bone with an expanded head.

These resemblances to booid snakes are numerous, clear, and detailed; we believe that they require *Dinilysia* to be placed in the booid complex close to *Anilius* and *Cylindrophis*.

Nevertheless, there are also a number of very primitive features, quite in keeping with the Cretaceous age of the fossil, that make *Dinilysia* more lizardlike than any other known snake. Generalized lizard features are: (1) frontal lappets under nasals, limiting nasofrontal mobility; (2) postfrontal and postorbital both present; (3) trigeminal foramen single; (4) exposure of the stapedial footplate (= absence of a crista circumfenestralis); (5) large, laterally-projecting convex basipterygoid processes; (6) palatines with deep choanal grooves and without anterior toothed projections; (7) posterior processes of pterygoids vertical plates, concave medially; (8) jugal present (but see below); (9) a single opening in the anterior braincase for olfactory tracts.

These primitive lizardlike features are again numerous enough and impressive enough that, if *Dinilysia* is related to boids and aniliids, it must belong rather far down in the ancestry of the booid complex.

In its lizardlike aspects, it must be emphasized, *Dinilysia* does not show special affinity to any group of lizards. The lizard characters cited above are generalized and are primitive for squamates; the more detailed resemblances seem casual and random, inviting the suspicion that they are merely convergent. There are some specific resemblances to *Lanthanotus* or *Varanus*: (1) a somewhat *Lanthanotus*-like crista tuberalis behind the posterior lacerate foramen; (2) a *Lanthanotus*-like curvature of the anterior (palatine) processes of the pterygoids; (3) prefrontals that intervene between maxillae and nasals. But these are balanced by the ways in which *Dinilysia* appears to be more primitive than *Lanthanotus* or *Varanus*; e.g. the deep choanal impressions on the palatines and participation of the maxilla in the suborbital fenestra (ways in which primitive snakes generally seem more primitive than *Lanthanotus*). There is neither special confirmation nor denial in our study for an anguimorph origin of snakes (*cf.* McDowell and Bogert, 1954). However, it is very possible that the expectation that *Dinilysia* will shed much light on snake origins is erroneous. It is perhaps already too close to extant groups of snakes to be helpful.

Yet, snake though it is and close though it seems to *Anilius* and *Cylindrophis*, there are aspects in which *Dinilysia* has provided wholly astonishing features. The strongly posterolaterally-produced paroccipital and supratemporal processes have been interpreted as an intermediate between lizard and snake conditions. If it is really an intermediate, it is one quite outside expectation. Beyond this, however, there are other aspects of *Dinilysia* that are special and unique: (1) the vomers *underlain* by anterior portions of the palatines; (2) the extraordinarily robust nasal septum; (3) the low position of the fenestra rotunda on the occiput; (4) the peculiar shape of the quadrate, as well as the oval quadrate-articular joint; (5) the almost incredible element that we call the jugal, and (6) the large supratemporal applied closely to the skull. These are so special, and are so far from being in any simple sense intermediate between lizard and snake, that *Dinilysia* seems likely to be off on its own side branch and away from the main line of the ancestry of modernized snakes. Related to booids it seems to be, and among these is closest to *Anilius* and *Cylindrophis*, yet it appears also to have been a very early and eccentrically divergent offshoot of this stock. Taxonomic expression of these conclusions need involve no change from that already given by Romer (1956: 570), who raised *Dinilysia* to family status and placed it at the base of the superfamily Booidea.

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ABBREVIATIONS

an = angular
art = articular
avc = anterior opening of vidian canal
bo = basioccipital
bp = basipterygoid process
bs = basisphenoid
ca = coronoid articulation surface
co = coronoid
cp = compound bone
de = dentary
ec = ectopterygoid
eo = exoccipital
f = unknown foramen
fo = fenestra ovalis
fp = foramen for palatine artery
fr = frontal
fro = fenestra rotunda
ju = jugal
lf = lacrimal foramen
mp = maxillopalatine foramen
mx = maxilla
na = nasal
oc = orbitonasal canal
of = optic fenestra
pa = parietal
pal = palatine
pf = postfrontal
plf = posterior lacerate foramen
po = postorbital
pr = prootic
pra = prearticular
prf = prefrontal
ps = parasphenoid
pt = pterygoid
pvc = posterior opening of vidian canal
qu = quadrate
s = stapes
sm = septomaxilla
so = supraoccipital
sot = spheno-occipital tuber
sp = splenial
st = supratemporal
sur = surangular
t = trabecular pit and groove
vo = vomer
V = trigeminal foramen
VII = facial foramen

Plate 1. *Dinilysia patagonica*; original plate from Woodward (1901); 1, dorsal and left lateral views of skull; 1b, ventral view of left maxilla showing tooth sockets; 1c, lateral view of left quadrate; 2, a portion of the vertebral column, dorsal view; all × 1. Abbreviations used on this original plate may not coincide with those on p. 62.

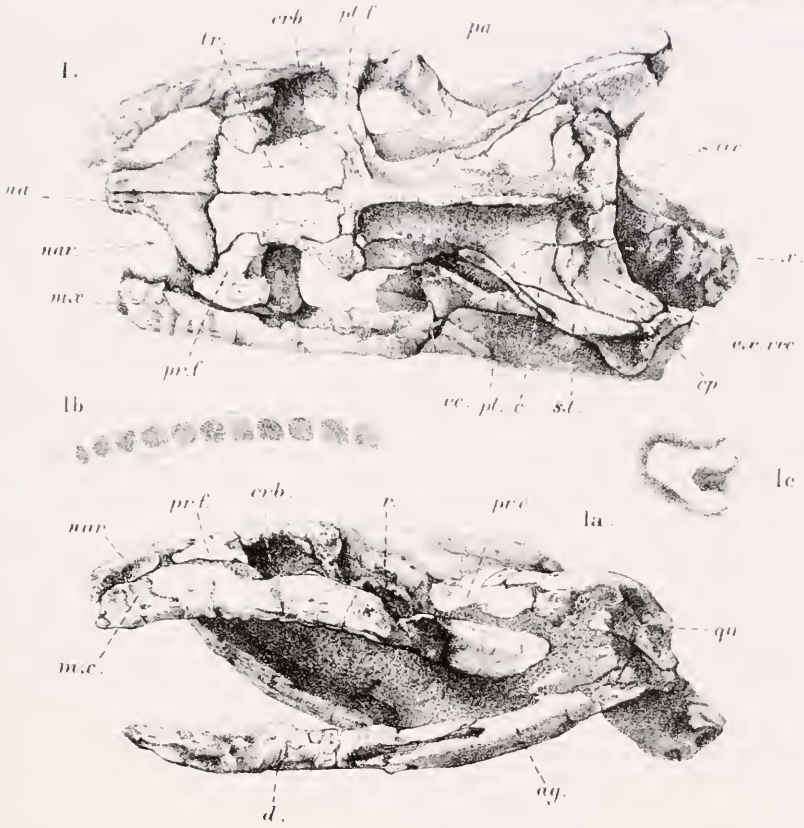
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Plate 2. *Dinilysia patagonica*; right lateral and ventral views of copy of British Museum (Natural History) cast of original specimen of *Dinilysia*. Note complete postorbital arch and complete maxilla. × 1.5.

Plate 3. *Dinilysia patagonica;* dorsal view of skull.

Plate 4. *Dinilysia patagonica*; ventral view of skull.

METRIC 1
2

Plate 5. *Dinilysia patagonica*; left lateral and occipital views of skull.

Bulletin OF THE
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The Lynx Spider Genus *Hamataliwa* in Mexico and Central America (Araneae: Oxyopidae)

ALLEN R. BRADY

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THE LYNX SPIDER GENUS *HAMATALIWA* IN MEXICO AND CENTRAL AMERICA (ARANEAE: OXYOPIDAE)

ALLEN R. BRADY[1]

ABSTRACT

Spiders of the genus *Hamataliwa* in Mexico and Central America are described and illustrated. A new definition of *Hamataliwa* includes eight species originally assigned to *Oxyopeidon* and seven species originally assigned to *Oxyopes*. Four species of *Hamataliwa* from Mexico and Central America are retained in the genus and five species are described as new. In short, 24 species of *Hamataliwa* are recorded from Mexico and Central America, where previously only four were reported. The genus *Hamataliwa*, undoubtedly, will prove to be as widespread as *Oxyopes* when additional studies in tropical regions are completed.

Three species groups of *Hamataliwa* have been established on the basis of positive correlation between eye arrangement and the structure of the palpus and/or epigynum. The *banksi* group consists of seven species, the *puta* group consists of eight species, and the *grisea* group consists of three species. On the basis of present information no clearly defined relationship could be established for the remaining six species of *Hamataliwa*.

Although distribution data are scarce, records and maps are given for those specimens examined. Much more work needs to be done in Mexico and Central America to provide a clear picture of species ranges. In general, intraspecific populations of oxyopids in this region tend to be much more variable than comparable groups from North America, north of Mexico.

INTRODUCTION

This paper is an outgrowth of an earlier work on the Oxyopidae of North America, north of Mexico (Brady, 1964). In that investigation 17 species of oxyopids representing three genera were recorded and described from North America. For that study, I examined numerous specimens of Neotropical oxyopids to determine the geographic range of the North American species. I uncovered problems of inadequate descriptions and figures, as well as numerous errors in systematic placement. The present study is primarily an effort to correct this situation and to establish a foundation on which future investigations might be based. The collections examined from Mexico and Central America were not extensive, and although collecting has been concentrated only in certain areas of this region (for example, Barro Colorado Island), I judged the amount of material adequate. Because the number of oxyopid species increases considerably as one moves southward into Mexico and Central America, it seemed advisable to report on the genera in this area individually rather than to treat the entire family in one monograph. This paper is the first in a series I plan on the Neotropical oxyopids. In addition to shedding some light on the

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evolutionary relationships of the species involved, I hope that this study will provide pertinent information about the distributional patterns of spiders in the Neotropical Region.

In the present investigation, I cover eight species found in Mexico and Central America that were originally described in the literature as *Oxyopeidon*. In addition, I have placed in *Hamataliwa* seven species originally assigned to *Oxyopes* and recorded from that region. These changes are based on an intensive study that necessitated a redefinition of *Hamataliwa* (Brady, 1964). This new diagnosis indicated both that *Oxyopeidon* was a synonym of *Hamataliwa* and that certain species placed in *Oxyopes* were much closer to *Hamataliwa* than investigators previously thought. Four species of *Hamataliwa* from Mexico and Central America remain in the genus, and five species are newly described in this paper. It is likely that numerous species of *Oxyopes* and the remaining species described in the literature under *Oxyopeidon* belong in *Hamataliwa* as characterized here. After additional studies are completed, the genus *Hamataliwa* will undoubtedly prove to be as widespread as *Oxyopes*. For example, in a recent work on spiders from south New Guinea, Father Chrysanthus (1967) figures *Oxyopes tapponiformis* Strand. The figures, as well as measurements provided by the author, indicate that this species belongs in *Hamataliwa*.

The revision of *Hamataliwa* as it is treated here is based primarily on morphological evidence. Although my approach to delimiting species is based on morphological distinctness, I have considered carefully other factors, such as ecological amplitude and individual variation demonstrated in field investigations of the North American species. I have used *Hamataliwa grisea* and *H. helia*, two of the more closely studied American representatives of this group, as "standards" for testing assumptions and for drawing conclusions about reproductive isolation. My preliminary studies of the behavior of these two species in the field and their natural history have been reported elsewhere (Brady, 1964). I have considered other factors which I do not yet fully understand. For example, it appears that members of a single population of the same species in Mexico and Central America tend to vary more than their North American counterparts. Perhaps this is a result of the increased interspecific competition among tropical populations, or it may simply be a consequence of local diversity in the physical environment. This intraspecific variation must, however, be considered in judging the significance of differences in allopatric populations.

In this day of molecular analysis and comparative behavioral studies, the value of a strict morphological approach to systematic problems may be questioned, but one must lay a foundation at some point. The time necessary to gather information to establish this base is a primary question. How long would it take to acquire enough ecological, behavioral, or molecular data so that one would have sufficient evidence to modify the conclusions drawn from morphology? For the Neotropical Oxyopidae, it would take months and perhaps years. I wish to make clear that I am not arguing against the acquisition of additional information from ecological, behavioral, and molecular studies, nor am I questioning the value of data from these areas. I hope that this paper might stimulate further investigations in ecology, behavior, and molecular analysis. I am emphasizing the need for presenting basic morphological revisions where adequate numbers of specimens are available and qualified systematists are present. I feel that morphological studies cognizant of the factors mentioned above provide an adequate basis for establishing genetic relationships and that such studies provide a firm foundation on which to build future interpretations of phylogeny. Because this

morphological study modifies considerably the findings of earlier authors, and because it clears up some difficult nomenclatural problems and consolidates scattered bits of information, I felt that it should be presented without further delay.

ACKNOWLEDGMENTS

I initiated this study in 1964 while I was a Research Fellow in Arachnology at the Museum of Comparative Zoology, Harvard University. This appointment was under the auspices of a grant from the Evolutionary Biology Committee. I am especially grateful to Dr. H. W. Levi of the Museum of Comparative Zoology, who has offered advice and aided in many ways the preparation of this paper. Collections from the Museum of Comparative Zoology were available throughout this investigation. Much of this material was collected by Dr. A. M. Chickering, and it is through his efforts in the field that the study became practicable. I am also indebted to Dr. W. J. Gertsch for collections from the American Museum of Natural History.

I wish to thank Dr. G. Owen Evans and Mr. Douglas Clark, whose hospitality I enjoyed for three weeks in the summer of 1963 at the British Museum (Natural History). A grant from the Evolutionary Biology Committee, Biological Laboratories, Harvard University, made this visit possible. Type specimens of O.P.- and F.O.P.-Cambridge were drawn and examined at that time. As my investigation progressed, I realized that critical measurements and additional drawings would be necessary to diagnose properly certain of the Cambridges' types. I appreciate the further courtesy of Dr. Evans and Mr. Clark for making this possible.

I would also like to thank Dr. O. Kraus of the Senckenberg Museum, Frankfurt, and Dr. E. Kritscher of the Natural History Museum, Vienna, for making available critical type specimens. Father Chrysanthus aided by checking the proper Latin endings for many of the specific names.

A 1967 Summer Faculty Grant from Hope College allowed much needed time for the preparation and writing of this paper. National Science Foundation Grant GB-13925 helped to defray expenses connected with this study.

METHODS

The methods for measuring specimens during this study were essentially the same as those I employed in my earlier paper on the family Oxyopidae (Brady, 1964). The color descriptions and illustrations are based on alcoholic specimens that were in reasonably good condition (except where noted to the contrary).

Locality records are listed geographically in a sequence from north to south and from east to west. The number of specimens collected at each locality is indicated; the lower case "o" represents immature specimens.

For most species, the face view as well as the dorsal view of a male and female were drawn (when both were available). A ventral external view of the epigynum (after all of the hair had been removed) was drawn. This drawing often reveals some internal structures through the integument. In addition, a dorsal internal view with the genitalia separated from the spider and submerged in clove oil was figured. The female genitalia of all species are drawn to the same scale. The scales are indicated on the plates. Two views, a ventral and a lateral, were drawn for each species. These were drawn after the palpus had been gently scraped free of hair to reveal as clearly as possible the palpal sclerites and patellar or tibial apophyses. No attempt was made to indicate spination or hairiness in the drawings. All palpi are drawn to the same scale.

SCIENTIFIC NAMES OF UNCERTAIN STATUS

R. V. Chamberlin (1924) described one new species and one new subspecies of *Oxyopeidon* from the shores and islands

of the Gulf of California. Immature specimens of *Oxyopeidon absolutum* were collected from San Esteban Island, Concepcion Bay, Puerto Escondido, Angel de la Guarda Island, and San Josef Island. There are no distinguishing characteristics that differentiate these specimens from immature *Hamataliwa grisea*. A geographic race, *Oxyopeidon absolutum obliquum* was described from Coronados Island because of different coloration than other specimens of *O. absolutum*. The holotype is an early instar of *Hamataliwa*. *Hamataliwa grisea* varies considerably in coloration, as do other species of *Hamataliwa*, and coloration alone does not warrant subspecific recognition. Until mature specimens are collected from the above localities along the shore and on islands of the Gulf of California, it seems best to consider *Oxyopeidon absolutum* as a synonym of *Hamataliwa grisea*.

Reimoser (1939) described two new species of *Hamataliwa* from San José, Costa Rica. One of these, *H. schmidti*, is newly described and figured in this study. The other species, *H. tristani*, is based on two female specimens supposedly deposited in the Natural History Museum, Vienna. These two specimens were unavailable for study, and the original description and Reimoser's sketch are not sufficient to provide an accurate determination of *H. tristani*.

Hamataliwa Keyserling

Hamataliwa Keyserling, 1887, Verh. Zool.-Bot. Ges. Wien, 6:458, fig. 24, ♀. Type species by monotypy: *Hamataliwa grisea* Keyserling, op. cit., 6:458, fig. 24, ♀, from North America in British Museum (Natural History), examined.

Oxyopeidon O. P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1: 139. Type species designated by F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:346: *Oxyopeidon putum* O.P.-Cambridge, 1894, *op. cit.*, 1:140, in British Museum (Natural History), examined.

Characteristics. For general characteristics of the genus refer to Brady (1964), p. 496.

Diagnosis. In *Hamataliwa* the eye rows differ in position and/or proportional width from those of *Oxyopes*. The face is often not vertical as it is in other oxyopids, but slopes more gradually toward the clypeus. In many species of *Hamataliwa*, the carapace is clothed with long hair, often with tufts in the eye region. In addition, there may be long hairs on the lateral surfaces of the legs and along the sides of the abdomen. These features add to the cryptic effect offered by their coloration and provide concealment against bark of trees and twigs or against woody shrubs. Many species are undoubtedly arboreal in habit. *Hamataliwa* seems to be as well defined ecologically as it is morphologically.

Leg development and structure appear to be correlated with arboreal habits. In all species studied, except *H. tricuspidata*, the relative leg length is I-II-III-IV. The first two pairs of legs are long and robust, the third and fourth pairs weakly developed. In *Oxyopes* the fourth pair of legs is strongly developed concomitant with their jumping habits. Observed species of *Hamataliwa* are more sedentary than *Oxyopes*.

The general form of the epigyna in *Hamataliwa* is a semi-circular or U-shaped, heavily sclerotized rim surrounding a shallow median depression with a characteristic shape in each species. Male palpi are also similar in basic construction, with the embolus following a definite route and forming a characteristic twist or loop near the base at the mesal edge of the cymbium.

The above combination of characteristics distinguish members of *Hamataliwa* from *Oxyopes*.

SPECIES GROUPS OF *HAMATALIWA*

Mexican and Central American species of *Hamataliwa* can be separated into several groups based on the comparative width of the eye rows and the position of certain eyes relative to others. I made comparisons of the structure of the geni-

talia, bodily proportions, and coloration of those species that have similarities in eye arrangement. Most species of *Hamataliwa* can be placed in species groups based on a positive correlation between eye arrangement and the structure of the palpus or epigynum. Color patterns and bodily proportions are also useful, but they are not as reliable in preserved specimens. Although the species groups thus established may not be strictly natural assemblages, they do include species that have certain common characteristics and are apparently related. A few species are arbitrarily included in a particular species group because of a similarity in eye arrangement. In these cases we know only one sex; the discovery of the other sex will determine whether or not the placement is valid.

Banksi group. In the *banksi* group (*banksi, helia, brunnea, triangularis, barroana, globosa* and *cheta*) the ALE row is wider than or subequal to the PME row. *Hamataliwa banksi, H. helia, H. brunnea,* and *H. triangularis* have the ALE row wider than the PME row. Of these four species, *H. banksi* and *H. helia* are very closely related (see discussion under *H. banksi*). *Hamataliwa brunnea* agrees closely with *H. banksi* and *H. helia* in eye arrangement (compare Fig. 39 with Fig. 3), but the epigynum of *H. brunnea* is different (compare Fig. 59 with Figs. 54–58). Although the epigynum of *H. triangularis* is quite distinct from that of other members of this group, the eye arrangement resembles that of *H. banksi* and the palpus of the male bears a close resemblance to that of *H. helia* (compare Figs. 120, 121 of this paper with figs. 130–133 of Brady, 1964).

Hamataliwa barroana, H. globosa, and *H. cheta* have the ALE row subequal to the PME, i.e. the PME row is less than .05 mm wider than the ALE. This eye arrangement is much nearer to that of members of the *banksi* group than to that of other species of *Hamataliwa.*

The epigynum and internal genitalia in *H. barroana* bear a strong resemblance to those of *H. banksi* (compare Figs. 60–62 with Figs. 54–58). *Hamataliwa cheta* has an epigynum similar to that of *H. barroana. Hamataliwa globosa* is included in this group because of the eye arrangement. The palpus of *H. globosa* (Figs. 122–123) distinguishes it from all other species of *Hamataliwa.*

Puta group. In the *puta* group (*puta, ursa, cavata, hista, flebilis, difficilis, laeta, crocata*), the PME row is much wider than the ALE row. These species have the PME much closer to the PLE than do the members of the *banksi* species group.

The male palpi also strongly resemble one another (see Figs. 107–118). *Hamataliwa puta, H. ursa,* and *H. cavata* have very similar epigyna (compare Figs. 65–67, with Figs. 68, 69 and Figs. 73, 74). These three species may prove to be geographic races after more data on their biology and distribution is collected. On the basis of present materials and information, however, they appear to be morphologically distinct species. In *H. puta* and *H. ursa,* the male palpi easily separate the two species (compare Figs. 113–119 with Figs. 111–112). The seminal receptacles of *H. cavata* are considerably more elongate than those in *H. puta* or *H. ursa* (compare Fig. 73 with 65, 68).

Hamataliwa flebilis and *H. laeta* have epigyna resembling those of *H. banksi,* but these may also be associated with *H. puta.* The male palpus of *H. flebilis* is similar to that of other males in the *puta* group (compare Figs. 124, 125 with Figs. 107–119). Because of this similarity and because of the correspondence in eye arrangement, *H. flebilis* and *H. laeta* are included in the *puta* group.

Hamataliwa hista has an epigynum readily distinguished from that in all other species of *Hamataliwa;* however, the male palpus bears a strong resemblance to that in other members of the *puta* species

group. (compare Figs. 107–108 with Figs. 109–119).

Hamataliwa difficilis and *H. crocata* are placed in the *puta* group primarily because of eye arrangement. Although their epigyna are distinct, they may arbitrarily be considered as similar to those of the *puta* complex. When the male of *H. difficilis* is known, it will be easier to place this species. *Hamataliwa crocata* has a distinct male palpus (Figs. 126, 127) and is the most divergent members of this species group.

Grisea group. The epigyna and internal genitalia of *H. grisea, H. facilis,* and *H. schmidti* bear a strong resemblance to one another. The eye relationships in this species group are not as uniform as are those in the previous two species groups, but the structure of the cephalothorax and the general arrangement of the eyes, together with the genitalic similarities, support their amalgamation into a separate complex. Discovery of the males in *H. facilis* and *H. schmidti* will clarify the situation.

Of the remaining six species, *H. positiva* and *H. unca* have eye arrangements and epigyna that closely resemble one another, thus indicating kinship, but they could not be linked with other species. *Hamataliwa positiva* has an epigynum resembling that in certain specimens of *H. facilis* (compare Fig. 93 with Figs. 97, 98); however, the eye arrangements in the two species are completely different (compare Fig. 43 with Fig. 44). *Hamataliwa circularis* and *H. subfacilis* have eye dispositions reminiscent of those in members of the *puta* species group, but they do not agree in proportion. The bodily structure and epigynum of *H. circularis* (Figs. 37, 38, 99, 100) and the eye arrangement and epigynum of *H. subfacilis* (Figs. 45, 92) make it difficult to relate them to any group.

The general body structure, profuse hair, and structure of the epigynum of *H. bufo,* as well as the absence of the male, exclude it from any of the above groups.

Hamataliwa tricuspidata is distinct from all species of *Hamataliwa* thus far studied. The order of leg length is I-II-IV-III, and coloration and eye arrangement resemble those in certain species of *Oxyopes,* but the epigynum and palpi, together with the proportions of the legs, are akin to those in *Hamataliwa* (see discussion under *H. tricuspidata*).

KEY TO SPECIES OF *HAMATALIWA*

MALES

1a. ALE row wider than or subequal* to PME row 2
1b. PME row distinctly wider than ALE row 5
2a. Cymbium of palpus almost as wide as long, ALE row subequal to PME. Color pattern and eye arrangement as in Figs. 11, 12. Palpus as in Figs. 122, 123 ..... *globosa*
2b. Cymbium of palpus much longer than wide, ALE row slightly wider than PME 3
3a. Distinct color pattern and eye arrangement as in Figs. 52, 53. Palpus as in Figs. 128, 129 ..... *tricuspidata*
3b. Color pattern not as in 3a. Palpus not resembling those in Figs. 128, 129 4
4a. Palpus illustrated in Figs. 120, 121. Color pattern and eye arrangement as in Figs. 9, 10 ..... *triangularis*
4b. Palpus illustrated in Figs. 130–133. Color pattern and eye arrangement as in figs. 124, 125 (Brady, 1964) ..... *helia*
5a. Palpus with two large tibial apophyses as in Figs. 126, 127. Color pattern and eye arrangement as in Figs. 35, 36 ..... *crocata*
5b. Palpus with only a single tibial apophysis or a lateral apophysis with a large tooth or spur at its base 6
6a. Palpus with a single lateral apophysis without a tooth or spur at its base 7
6b. Palpus with a single lateral apophysis with a conspicuous tooth or spur at its base as in Figs. 107–119 8
7a. Palpus illustrated in Figs. 124, 125. Color pattern and eye arrangement as in Figs. 25, 26 ..... *flebilis*
7b. Palpus illustrated in Figs. 128, 129. Color pattern and eye arrangement as in figs. 122, 123 (Brady, 1964) ..... *unca*
7c. Palpus illustrated in Figs. 134, 135.

* PME row less than .05 mm wider than ALE row.

Color pattern as in figs. 126, 127 (Brady, 1964) ..... *grisea*

8a. Palpus illustrated in Figs. 107, 108. Color pattern and eye arrangement as in Figs. 27, 28 ..... *hista*

8b. Palpus illustrated in Figs. 109, 110. Color pattern and eye arrangement as in Figs. 29, 30 ..... *cavata*

8c. Palpus illustrated in Figs. 111, 112. Color pattern and eye arrangement as in Figs. 31, 32 ..... *ursa*

8d. Palpus illustrated in Figs. 113–119. Color pattern and eye arrangement as in Figs. 33, 34 ..... *puta*

KEY TO SPECIES OF *HAMATALIWA*

FEMALES

1a. ALE row wider than or subequal* to PME row 2

1b. PME row distinctly wider than ALE row 6

2a. Patella-tibia IV slightly longer than patella-tibia III. Distinctive contrasting color pattern as illustrated in Figs. 50, 51. Epigynum and internal genitalia as in Figs. 104–106. ..... *tricuspidata*

2b. Patella-tibia III slightly longer than patella-tibia IV. Color pattern not as in 2a 3

3a. ALE row subequal to PME row, AME touching a line drawn tangent to lower edge of ALE, and AME less than own diameter from ALE on same side 4

3b. ALE row slightly but distinctly wider than PME row, AME well below a line drawn tangent to lower edge of ALE, and AME at least its own diameter from ALE on same side 5

4a. Epigynum and internal genitalia as in Figs. 60–62. Color pattern and eye arrangement as in Figs. 5, 6 ..... *barroana*

4b. Epigynum and internal genitalia as in Figs. 63, 64. Color pattern and eye arrangement as in Figs. 1, 2 ..... *cheta*

5a. Epigynum as in Fig. 59. Face view as in Fig. 39 ..... *brunnea*

5b. Epigynum and internal genitalia as in Figs. 54–58. Color pattern and eye arrangement as in Figs. 3, 4 ..... *banksi*

5c. Epigynum and internal genitalia as in Figs. 119, 120. Color pattern and eye arrangement as in figs. 112–114 (Brady, 1964) ..... *helia*

5d. Epigynum and internal genitalia as in Figs. 81–84. Color pattern and eye arrangement as in Figs. 7, 8 ..... *triangularis*

6a. Line drawn tangent to lower edge of ALE running above AME row. Epigynum and internal genitalia as in Figs. 101–103. Color pattern as in Figs. 48, 49 ..... *bufo*

6b. Line drawn tangent to lower edge of ALE running below AME, running through AME, or tangent to the upper edge 7

7a. Line drawn tangent to lower edge of ALE running below center of AME 8

7b. Line drawn tangent to lower edge of ALE, tangent to upper edge of AME, or running above center of AME 9

8a. Face view as in Fig. 44. Epigynum and internal genitalia as in Figs. 94–98 ..... *facilis*

8b. Epigynum as in Figs. 89–91. Color pattern and eye arrangement as in Figs. 46, 47 ..... *schmidti*

8c. Epigynum as in Figs. 115, 116. Color pattern as in figs. 108, 109 (Brady, 1964) ..... *grisea*

9a. AME more than own diameter from ALE 10

9b. AME own diameter or less from ALE 11

10a. Face view as in Fig. 43. Epigynum as in Fig. 93 ..... *positiva*

10b. Epigynum and internal genitalia as in Figs. 77, 78. Color pattern and eye arrangement as in Figs. 23, 24 ..... *crocata*

10c. Epigynum and internal genitalia as in Figs. 73, 74. Color pattern and eye arrangement as in Figs. 17, 18 ..... *cavata*

11a. Posterior sclerotized rim of epigynum more or less U-shaped 15

11b. Posterior sclerotized rim of epigynum V-shaped, scalloped, or straight 12

12a. Posterior rim of epigynum scalloped or V-shaped 13

12b. Posterior rim of epigynum straight, median depression rectangular 14

13a. Posterior rim of epigynum scalloped as in Fig. 92. Face view as in Fig. 45 ..... *subfacilis*

13b. Posterior rim of epigynum V-shaped as in Figs. 70–72. Color pattern and eye arrangement as in Figs. 13, 14. ..... *flebilis*

14a. Epigynum and internal genitalia as in Figs. 85–88. Face view as in Figs. 40, 41 ..... *difficilis*

14b. Epigynum and internal genitalia as in Figs. 117, 118. Color pattern and eye arrangement as in figs. 110, 111 (Brady, 1964) ..... *unca*

15a. Posterior rim of epigynum broadly U-shaped, almost circular; seminal receptacles widely separated as in Figs. 99–100. Color pattern and eye arrangement as in Figs. 37, 38 ..... *circularis*

* PME row less than .05 mm larger than ALE.

MAP 1

15b. Posterior rim U-shaped, seminal receptacles close together as in Figs. 65–72 16
16a. Epigynum and internal genitalia as in Figs. 65–67. Color pattern and eye arrangement as in Figs. 21, 22. ..... *puta*
16b. Epigynum and internal genitalia as in Figs. 68, 69. Color pattern and eye arrangement as in Figs. 19, 20 ..... *ursa*
16c. Epigynum and internal genitalia as in Figs. 73, 74. Color pattern and eye arrangement as in Figs. 17, 18 ..... *cavata*
16d. Epigynum and internal genitalia as in Figs. 75, 76. Color pattern and eye arrangement as in Figs. 15, 16 ..... *hista*

SPECIES DESCRIPTIONS

Hamataliwa banksi (Mello-Leitão)

Figures 3, 4, 54–58. Map 1.

Oxyopes brevis Banks, 1898, Proc. California Acad. Sci., 1(7):278, pl. 17, fig. 26, ♀. Female lectotype, here designated, from Cerro del Taste, Territorio Sur, Baja California, in Museum of Comparative Zoology, examined. Name preoccupied, not *Oxyopes brevis* Thorell, 1881.

Oxyopes annulipes F.O.P-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea 2:345, pl. 32, fig. 27, ♀. Female holotype from Amula, 9.5 km NW of Chilapa, Guerrero, Mexico, in the British Museum (Natural History), examined. Name preoccupied, not *Oxyopes annulipes* Thorell, 1892. NEW SYNONYMY.

Oxyopes banksi Mello-Leitão, 1928, Bol. Mus. Rio de Janeiro, 4(3):50. New name for *Oxyopes brevis* Banks.

Oxyopes cambridgei Mello-Leitão, 1928, Bol. Mus. Rio de Janeiro 4(3):50. New name for *Oxyopes annulipes* F.O.P.-Cambridge. NEW SYNONYMY.

Discussion. Coincidentally, the names *Oxyopes brevis* and *Oxyopes annulipes*, applied to this species by Banks and F.O.P.-Cambridge respectively, were both preoccupied. Mello-Leitão (1928) noticed this and gave new names to the species. The two names are considered synonymous in this paper because only one species is involved (compare Figs. 54–57 with Fig. 58).

Measurements. Length of eight females 4.1–5.1 mm, mean 4.84 mm; carapace width 1.4–2.0 mm, mean 1.76 mm; carapace length 1.7–2.5 mm, mean 2.16 mm.

Width of eye rows: AME .25–.30 mm, mean .272 mm; ALE .50–.68 mm, mean .631 mm; PLE .88–1.13 mm, mean 1.025 mm; PME .45–.63 mm, mean .547 mm.

Segments of leg I (five females): femur 1.9–2.4 mm, mean 2.18 mm; patella-tibia 2.0–2.7 mm, mean 2.43 mm; metatarsus 1.4–1.6 mm, mean 1.51 mm; tarsus .8–.9 mm, mean .82 mm; total length I 5.9–7.5 mm, mean 6.94 mm.

Length of patella-tibiae: II 1.9–2.5 mm, mean 2.23 mm; III 1.4–1.9 mm, mean 1.72 mm; IV 1.3–1.9 mm, mean 1.59 mm.

Color. Female. Pattern illustrated in Figures 3 and 4. Face pale yellow to light orange, chelicerae with slightly darker orange tint. Lighter, inversely T-shaped mark from AME row to lower edge of clypeus. Flattened white hairs, heaviest in eye region and along sides of face.

Carapace pale orange to orange, with scattered spatulate-shaped white hairs, most abundant along sides and at posterior declivity.

Dorsum of abdomen cream. Venter pale yellow to cream without distinct median stripe.

Legs pale yellow to light orange, somewhat darker distally.

Labium, endites, and sternum pale yellow to light orange.

Diagnosis. Hamataliwa banksi is very close to *H. helia* in body dimensions, eye arrangement, and the shape of the epigynum. These two species apparently overlap in distribution.

Hamataliwa banksi is larger than *H. helia*, and the females can be distinguished by epigynal structure. In *H. helia* the posterior rim of the epigynum is not as heavily sclerotized, and the central depression of the epigynum is larger and more oval than it is in *H. banksi* (compare figs. 119–120 of Brady, 1964, with Figs. 54–58 of this paper).

Separation of these two species may become impossible after larger series of specimens are collected. Until males of *H. banksi* are found and are compared with *H. helia* males, it seems best to maintain them as separate species.

Distribution. Mexico and Central America (Map 1).

Records. MEXICO. *Baja California.* Territorio Sur, Cerro del Taste, ♀♀. *Guerrero.* Amula, 9.5 km NW of Chilapa, (H. H. Smith).

GUATEMALA. Cobán, July 1947, ♀ (C., P. Vaurie).

COSTA RICA. San José, ♀♀ (E. Schmidt).

Hamataliwa helia (Chamberlin)

Oxyopes helius Chamberlin, 1929, Ent. News, 40:19, fig. 4, ♀. Female holotype from Mixson's Hammock, Okefenokee Swamp, Georgia, in the American Museum of Natural History, examined.

Hamataliwa helia is closely related to *H. banksi* and may be synonymous with that species (see discussion under *H. banksi*).

For illustrations of the color patterns and genitalia and locality records, refer to Brady (1964, p. 497).

Distribution. Florida to Texas and south to Yucatan.

Hamataliwa brunnea (F.O.P.-Cambridge)

Figures 39, 59. Map 1.

Oxyopes brunneus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:346, pl. 32, fig. 29, ♀. Female holotype from Atoyac, Veracruz, Mexico, in the British Museum (Natural History), examined.

Discussion. This species is represented by the unique female above. Specimens designated as *Oxyopes brunneus* F.O.P.-Cambridge in other collections did not agree specifically with this one. The holotype was in such poor condition that the original color description is used below and only partial measurements were possible. Drawings of the epigynum and face were made.

Measurements. Length of female holotype 6.2 mm, carapace width 2.0 mm, carapace length 2.5 mm.

Width of eye rows: AME .28 mm, ALE .69 mm, PLE 1.22 mm, PME .62 mm.

Segments of leg I: femur 2.7 mm, patella-tibia 3.2 mm, metatarsus 1.9 mm, tarsus 1.0 mm, total length 8.8 mm.

Length of patella-tibiae: II 3.0 mm, III 2.0 mm, IV not present.

Color. Following is the original description of the holotype by F.O.P.-Cambridge: "The scales have been almost entirely rubbed off from the single specimen received of this species, and with these the colour and pattern have vanished; but the form of the vulva is quite distinct from that of any other *Oxyopes* in the collection before me. The general ground-colour is deep brown, whereas that of all the other members of the genus here described is yellow or orange."

Diagnosis. The structure of the epigynum in *H. brunnea* is similar to that of *H. crocata* (compare Fig. 59 with Fig. 78), but the eye arrangement in these two species is quite different (compare measurements). Body size and eye arrangement of *H. brunnea* ally it with *H. banksi.*

Record. MEXICO. *Veracruz.* Atoyac, ♀ (H. H. Smith).

Hamataliwa triangularis (Kraus)
Figures 7–10, 81–84. Map 1.

Oxyopes globosus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:343 (in part), pl. 32, figs. 19, 19a ♀ only. Female allotype, from *Bugaba, Panama, in the British Museum (Natural History), examined. Not *Oxyopes globosus* F.O.P.-Cambridge ♂ holotype.

Oxyopeidon triangularis Kraus, 1955, Abh. Senckenb. Naturf. Ges., 493:38, pl. 5, fig. 97. Female holotype from San Salvador, El Salvador, in Senckenberg Museum, examined.

Discussion. The female described by F.O.P.-Cambridge as *Oxyopes globosus* does not agree in size or eye arrangement with the male holotype. In all species of *Hamataliwa* investigated the males are smaller than the females. The male holotype of *O. globosus* is larger than 20 females of *O. globosus* F.O.P.-Cambridge that were measured. In addition the ALE row of the male holotype is not wider than the PME row as in the female. Therefore, *H. triangularis* (Kraus) becomes the valid name for the female described as *Oxyopes globosus* F.O.P.-Cambridge.

Measurements. Length of two males 3.8, 4.2 mm, carapace width 1.5, 1.6 mm, carapace length 1.8, 1.9 mm.

Width of eye rows: AME .25, .27 mm, ALE .53, .55 mm, PLE .87, .93 mm, PME .50, .53 mm.

Segments of leg I: femur 2.0, 2.1 mm, patella-tibia 2.5, 2.8 mm, metatarsus 1.7, 1.9 mm, tarsus .9, 1.0 mm, total length 7.1, 7.8 mm.

Length of patella-tibiae: II 2.4, 2.5 mm, III 1.8, 1.9 mm, IV – –*, 1.6 mm.

Length of 10 females 4.2–5.3 mm, mean 4.90 mm; carapace width 1.6–1.9 mm, mean 1.78 mm; carapace length 2.0–2.3 mm, mean 2.4 mm.

Width of eye rows: AME .27–.30 mm, mean .281 mm; ALE .57–.63 mm, mean .606 mm; PLE .97–1.03 mm, mean 1.005 mm; PME .53–.60 mm, mean .569 mm.

Segments of leg I: femur 2.2–2.5 mm, mean 2.40 mm; patella-tibia 2.7–3.0 mm, mean 2.85 mm; metatarsus 1.8–2.0 mm, mean 1.92 mm; tarsus .8–1.0 mm, mean .91; total length 7.7–8.4 mm, mean 8.08 mm.

Length of patella-tibiae: II 2.5–2.8 mm, mean 2.68 mm; III 1.9–2.3 mm, mean 2.07; IV 1.6–1.9 mm, mean 1.78 mm.

Color. Male. Pattern illustrated in Figures 9 and 10. Face and chelicerae yellow-orange. Distal ends of chelicerae lighter, yellowish. Cymbia of palpi brown.

Carapace yellow-orange to orange.

Dorsum of abdomen cream colored. Sides darker, brownish. Venter of abdomen cream colored, slightly darker medially.

Legs yellow-orange without dusky markings.

Labium and endites ivory to pale cream. Sternum ivory.

Color. Female. Pattern illustrated in Figures 7 and 8. Face and chelicerae yellow to yellow-orange, with relatively thick clothing of white appressed hairs, thickest at lateral and ventral margins of face.

* Chiriquí, 22 km NW of David.

* Two dashes indicate a missing leg segment.

Carapace pale yellow to yellow-orange. Vertical sides with white or mixture of white and dark brown spatulate hairs.

Dorsum of abdomen cream colored, without darker markings or, in a few specimens, an irregular spotted pattern formed from an intermixture of white and dark brown hairs. Large dark brown spots along sides of abdomen about one-third of the distance from the spinnerets to the base in these hirsute specimens. Venter of abdomen cream colored.

Legs pale yellow to cream with dusky brown bands at distal ends of femora and tibiae, tibiae dusky at proximal ends as well. Dusky bands formed by spatulate-shaped hair.

Labium and endites pale yellow to yellow-orange. Sternum cream to pale yellow.

Diagnosis. *Hamataliwa triangularis* is similar to *H. banksi* and *H. brunnea* in eye arrangement. The palpus of the male resembles that of *H. helia* (compare Figs. 120–121 of this paper with figs. 130–133 of Brady, 1964). *Hamataliwa triangularis* can be readily differentiated from other members of this group of species by the structure of the epigynum (Figs. 81–84).

Distribution. El Salvador to Panama (Map 1).

Records. EL SALVADOR. San Salvador, 21 June 1951, 3♀♀ (A. Zilch).

PANAMA. *Canal Zone.* Barro Colorado Island, numerous ♂♂♀♀ (A. M. Chickering); Madden Dam, 8 Aug. 1939, ♀ (A. M. Chickering), 28 May 1956, ♀ (W. E. Lundy).

Hamataliwa barroana (Chamberlin and Ivie)

Figures 5, 6, 60–62. Map 1.

Oxyopes barroanus Chamberlin and Ivie, 1936, Bull. Univ. Utah, Biol. Ser., 3(5):18, pl. 4, fig. 27, ♀. Female holotype from Barro Colorado Island, Panama Canal Zone, in the American Museum of Natural History, examined.

Measurements. Length of 10 females 4.7–5.7 mm, mean 5.16 mm; carapace width 1.7–1.9 mm, mean 1.81 mm; carapace length 2.1–2.3 mm, mean 2.19 mm.

Width of eye rows: AME .25–.28 mm, mean .274 mm; ALE .68–.73 mm, mean .708 mm; PLE 1.17–1.25 mm, mean 1.211 mm; PME .68–.77 mm, mean .730 mm.

Segments of leg 1: femur 2.0–2.4 mm, mean 2.17 mm; patella-tibia 2.5–3.0 mm, mean 2.72 mm; metatarsus 1.5–1.9 mm, mean 1.74 mm; tarsus .8–.9 mm, mean .82 mm; total length I 6.8–8.0 mm, mean 7.44 mm.

Length of patella-tibiae: II 2.4–2.6 mm, mean 2.48 mm; III 1.8–2.0 mm, mean 1.88 mm; IV 1.7–1.9 mm, mean 1.81 mm.

Color. Female. Pattern illustrated in Figures 5 and 6. Face yellow-orange with broad light brown vertical stripes from ALE to lower edge of clypeus. Chelicerae yellow-orange, overlaid with brown. Hexagonal area bounded by eyes, reddish. Interior distal ends lighter in color.

Carapace yellow-orange. Dorsum of abdomen cream colored. Cardiac area translucent gray. Lateral areas with scattered spots of reddish hair. Venter of abdomen cream colored with broad light brown stripe from epigastric furrow to base of spinnerets.

Legs pale yellow to cream.

Labium pale orange-yellow. Endites pale orange-yellow, distal ends tipped with cream. Sternum cream.

Diagnosis. *Hamataliwa barroana* is readily distinguished from other species of *Hamataliwa* by the shape of the epigynum. (Figs. 60–62). In both *H. barroana* and *H. globosa,* the ALE row is subequal to the PME row. They may be related to the *H. banksi* group in which the ALE row is wider than the PME rows. In all other species of *Hamataliwa*, the PME row is much wider than the ALE row, with the exception of *H. tricuspidata.*

Distribution. Mexico and Central America.

Records. MEXICO. *Veracruz.* La Buena Ventura, July 1909, ♀. *Yucatan,* Colonia, 13–19 Aug. 1952, ♀ (J., D. Pallister).

PANAMA. *Canal Zone.* Barro Colorado Island, numerous ♀♀, various collectors;

Gamboa, 11 Aug. 1939, 4♀♀; Madden Dam, 18 Aug. 1936, 4♀♀ (A. M. Chickering).

Hamataliwa globosa (F.O.P.-Cambridge)

Figures 122, 123. Map 1.

Oxyopes globosus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:343 (in part), pl. 32, figs. 18, 18a–c, ♂ only. Male holotype from Bugaba, Panama, in British Museum (Natural History), examined.

Discussion. The female described by F.O.P.-Cambridge as *Oxyopes globosus* belongs to the species described by Kraus (1955) as *Oxyopes triangularis*. For further comments see the discussion under *Hamataliwa triangularis*.

Measurements. Length of five males 4.7–5.5 mm, mean 4.92 mm; carapace width 1.8–1.9 mm, mean 1.85 mm; carapace length 2.1–2.4 mm, mean 2.18 mm.

Width of eye rows: AME .25–.28 mm, mean .264 mm; ALE .63–.72 mm, mean .668 mm; PLE 1.10–1.25 mm, mean 1.149 mm; PME .65–.75 mm, mean .685 mm.

Segments of leg I: femur 2.1–2.4 mm, mean 2.19 mm; patella-tibia 2.7–3.0 mm, mean 2.84 mm; metatarsus 1.9–2.0 mm, mean 1.91 mm; tarsus .9–1.0 mm, mean .92 mm; total length I 7.6–8.3 mm, mean 7.86 mm.

Length of patella-tibiae: II 2.4–2.7 mm, mean 2.57 mm; III 1.9–2.2 mm, mean 1.97 mm; IV 1.7–2.0 mm, mean 1.80 mm.

Color. Male. Pattern illustrated in Figures 11 and 12. Face yellow with broad vertical stripes of brown from ALE row to lower edge of clypeus. Chelicerae darker, brownish. Cymbia of pedipalpi dark brown.

Carapace light orange-yellow without darker markings or sometimes dusky along sides.

Dorsum of abdomen white to cream colored with brownish margins and sides. Often with a few scattered darker spatulate hairs about mid-point of abdomen. Venter of abdomen white to cream colored with or without median dusky band.

Legs yellow without darker markings.

Labium and endites yellow with distal ends lighter, ivory. Sternum ivory.

Diagnosis. Hamataliwa globosa is distinct from all other species of *Hamataliwa* on the basis of palpal structure (Figs. 122, 123). The fact that the cymbium of the palpus is almost as wide as it is long makes for easy recognition. The eye arrangement is nearest to that of *H. triangularis* and *H. barroana*.

Distribution. Mexico and Central America (Map 1).

Records. MEXICO. *San Luis Potosí.* Tamazunchale, 20 May 1952, ♂ (M. Cazier, W. Gertsch, R. Schrammel).

PANAMA. *Canal Zone.* Barro Colorado Island, 7–8 May 1946, 3♂♂ (T. C. Schneirla); Bugaba (Chiriquí, 22 km NW of David), ♂ (G. C. Champion).

Hamataliwa cheta sp. n.

Figures 1, 2, 63, 64. Map 1.

Holotype. Female from Cobán, Guatemala, July 1947 (C., P. Vaurie), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Measurements. Length of three females 6.4, 6.9, 7.5 mm; carapace width 2.3, 2.3, 2.4 mm; carapace length 2.8, 2.8, 2.9 mm.

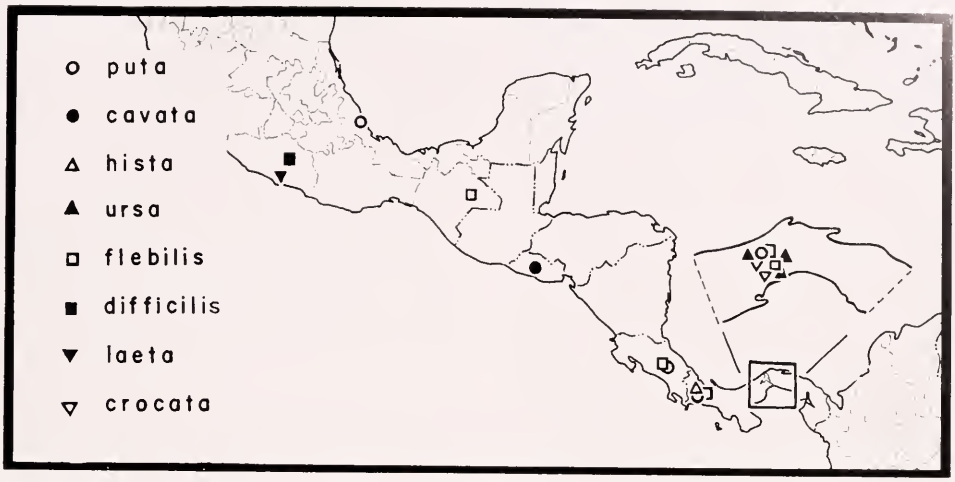
Width of eye rows: AME .28, .28, .30 mm; ALE .69, .72, .72 mm; PLE 1.20, 1.22, 1.27 mm; PME .70, .74, .75 mm.

Segments of leg I: femur 2.5, 2.7, 2.7 mm; patella-tibia 3.3, 3.5, 3.5 mm; metatarsus 2.0, 2.0, 2.1 mm; tarsus 1.0, 1.0, 1.0 mm; total length I 8.8, 9.2, 9.3 mm.

Patella-tibiae: II 2.9, 3.1, 3.1 mm; III 2.4, 2.5, – – mm; IV 2.3, 2.3, 2.4 mm.

Color. Female. Pattern illustrated in Figures 1 and 2. Face yellow-orange to orange-brown, lower edge of clypeus yellowish. Chelicerae yellow-orange to orange-brown with tuft of white hairs along inner margins of basal segments.

Carapace yellow-orange to orange-brown with darker brown hairs along vertical sides.



MAP 2

Dorsum of abdomen white to cream with cardiac area translucent white. Lateral areas darker brown. Venter of abdomen cream to pale yellow with broad median dusky stripe from epigastric furrow to base of spinnerets, margined by thin pale yellow stripe laterally.

Legs cream to pale yellow with metatarsi and tarsi darker, brownish.

Labium and endites pale yellow-orange, distal ends ivory. Sternum yellow.

Diagnosis. In *H. cheta* the PME row is subequal to the ALE row in width and the AME are well below the ALE (see Fig. 1) as in the *banksi* species group. The shape of the epigynum also conforms generally to that of *H. barroana*. For these reasons *H. cheta* is considered a member of the *banksi* species group. This species is easily distinguished from *H. barroana* and other species of the *banksi* group by its larger size and the structure of the epigynum (Figs. 63, 64).

Distribution. Guatemala (Map 1).

Records. GUATEMALA. Cobán, July 1947, 3♀♀ (C., P. Vaurie).

Hamataliwa puta (O.P.-Cambridge)

Figures 21, 22, 33, 34, 65–67, 113–119. Map 2.

Oxyopeidon putum O.P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:140, pl. 16, figs. 7, 7a–e, 8, 8a–c, ♂♀. Male lectotype, here designated, from Bugaba, Panama, in British Museum (Natural History) examined. F.O.P.-Cambridge, 1902, *op. cit.*, 2:347.

Measurements. Length of six males 4.7–5.3 mm, mean 5.04 mm; carapace width 1.8–2.2 mm, mean 1.93 mm; carapace length 2.1–2.5 mm, mean 2.23 mm.

Width of eye rows: AME .25–.27 mm, mean .256 mm; ALE .70–.75 mm, mean .737 mm; PLE 1.30–1.42 mm, mean 1.350 mm; PME .92–.99 mm, mean .960 mm.

Segments of leg I: femur 2.4–2.8 mm (5), patella-tibia 3.3–3.5 mm (3), metatarsus 2.1–2.5 mm (3), tarsus 1.0–1.2 mm (2), total length I 8.9–9.9 mm (2).

Length of patella-tibiae: II 2.6–3.4 mm (3), III 1.9–2.6 mm (3), IV 1.9–2.3 mm (3).

In most cases a leg or leg segment was missing, so for these particular measurements only the range is given, with the number of specimens in parentheses.

Length of ten females 4.7–6.1 mm, mean 5.36 mm; carapace width 1.6–2.0 mm, mean 1.79 mm; carapace length 2.0–2.4 mm, mean 2.18 mm.

Width of eye rows: AME .22–.28 mm, mean .254 mm; ALE .70–.80 mm, mean .746 mm; PLE 1.30–1.50 mm, mean 1.363 mm; PME .95–1.07 mm, mean .985 mm.

Segments of leg I: femur 2.0–2.4 mm, mean 2.18 mm; patella-tibia 2.5–2.9 mm, mean 2.68 mm; metatarsus 1.5–1.8 mm, mean 1.64 mm; tarsus .7–.9 mm, mean .80 mm; total length I 6.7–7.8 mm, mean 7.29 mm.

Length of patella-tibiae: II 2.2–2.8 mm, mean 2.45 mm; III 1.6–2.0 mm, mean 1.79 mm; IV 1.5–1.9 mm, mean 1.69 mm.

Color. Male. Pattern illustrated in Figures 33 and 34. In one male in good condition, the face and chelicerae are yellow-orange and clothed with white spatulate hairs. The sides of the face above the cheliceral articulation are darker brown. In rubbed specimens the face and chelicerae are orange-brown, with the lower edge of the clypeus and distal ends of chelicerae lighter. Palpi dark brown.

Carapace orange to orange-brown with darker brown hairs along sides.

Dorsum of abdomen pale yellow to cream. Venter pale yellow to cream without darker median stripe.

Legs pale yellow to yellow-orange.

Sternum cream to yellow-orange or amber. Labium and endites pale yellow to orange, cream distally.

Female. Pattern illustrated in Figures 21 and 22. Face and chelicerae orange-brown, usually with lighter cream color along lower edge of clypeus and sometimes at distal ends of chelicerae.

Carapace orange-brown. Dorsum of abdomen cream colored to tan with scattered patches of brown spatulate hairs. Venter cream to pale yellow. No darker markings.

Legs yellow to yellow-orange.

Labium and endites yellow to light orange, distal ends paler. Sternum cream to yellow.

Diagnosis. Hamataliwa puta is closely related to *H. ursa.* The structure of the epigyna and the female genitalia is very similar (compare Figs. 65–67 with Figs. 68–69), but the tibial apophysis of the palpus in *H. ursa* is much larger than it is in *H. puta* (compare Figs. 111–112 with Figs 113–119). For further discussion see the diagnosis of *H. ursa.*

Distribution. Mexico and Central America (Map 2).

Records. MEXICO. *Veracruz.* Veracruz, ♂ (N. Banks).

COSTA RICA. Antonios, ♂ (N. Banks).

PANAMA. Bugaba (Chiriquí, 22 km NW of David), ♂♂:10♀♀ (C. G. Champion). *Canal Zone.* Barro Colorado Island, 31 July 1954, ♂ (A. M. Chickering).

Hamataliwa ursa sp. n.

Figures 19, 20, 31, 32, 68, 69, 111, 112. Map 2.

Holotype. Male from Barro Colorado Island, Panama Canal Zone. June 1950 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is a noun in apposition meaning bear.

Measurements. Length of nine males 4.4–5.0 mm, mean 4.74 mm; carapace width 1.7–2.0 mm, mean 2.19 mm; carapace length 2.0–2.4 mm, mean 2.19 mm.

Width of eye rows: AME .22–.25 mm, mean .239 mm; ALE .65–.75 mm, mean .705 mm; PLE 1.19–1.39 mm, mean 1.306 mm; PME .87–.97 mm, mean .926 mm.

Segments of leg I: femur 2.1–2.6 mm, mean 2.39 mm; patella-tibia 2.7–3.3 mm, mean 2.99 mm; metatarsus 1.8–2.2 mm, mean 2.01 mm; tarsus .9–1.0 mm, mean .96 mm; total length 7.5–8.9 mm, mean 8.36 mm.

Length of patella-tibiae: II 2.4–3.0 mm, mean 2.73 mm; III 1.9–2.2 mm, mean 2.06 mm; IV 1.8–2.0 mm, mean 1.87 mm.

Length of ten females 5.3–6.7 mm, mean 6.04 mm; carapace width 1.9–2.2 mm, mean 2.02 mm; carapace length 2.3–2.6 mm, mean 2.43 mm

Width of eye rows: AME .27–.30 mm, mean .277 mm; ALE .78–.85 mm, mean .815 mm; PLE 1.45–1.64 mm, mean 1.536 mm; PME 1.02–1.19 mm, mean 1.102 mm.

Segments of leg I: femur 2.4–2.7 mm, mean 2.48 mm; patella-tibia 2.9–3.5 mm,

mean 3.13 mm; metatarsus 1.8–2.0 mm, mean 1.84 mm; tarsus .8–1.0 mm, mean .88 mm; total length I 7.9–9.2 mm, mean 8.33 mm.

Length of patella-tibiae: II 2.7–3.0 mm, mean 2.82 mm; III 1.9–2.2 mm, mean 2.02 mm; IV 1.8–2.1 mm, mean 1.91 mm.

Color. Male. Pattern illustrated in Figures 31 and 32. Coloration very similar to that of the female. In the male illustrated there are more brown spatulate hairs along the sides of the abdomen than in the female. Cymbia of palpi brown.

Color. Female. Pattern illustrated in Figures 19 and 20. Face and chelicerae yellow-orange to brownish orange, overlaid with darker hairs. White spatulate hairs at sides of face, thinning anteriorly. Lower edge of clypeus with yellowish tinge.

Carapace yellow-orange overlaid with brown spatulate hairs imparting a brownish orange tint. Darker along vertical sides.

Dorsum of abdomen cream to yellow with scattered patches of brown hair. Brown indentations about one-third of the distance from spinnerets to base of abdomen. Cardiac region and sometimes muscle depressions well marked. Venter cream to yellow with only a faint broad dusky stripe from epigastric furrow to base of spinnerets.

Legs yellow with darker brown spatulate hairs.

Labium yellow to light brown. Endites cream to yellow. Sternum ivory to cream.

Diagnosis. Hamataliwa ursa is very similar to *H. puta* in body size, leg length, and eye arrangement (compare measurements of these components). However, the epigynum of *H. ursa* is more broadly rounded than that of *H. puta* (compare Fig. 69 with Fig. 66) and the tibial apophysis of the male palpus in *H. ursa* is considerably larger than that in *H. puta* (compare Figs. 111–112 with Figs. 113–119).

The internal genitalia of the females are very much alike (compare Fig. 68 with Fig. 65); this similarity may be considered as good evidence for conspecificity. Males of *H. ursa*, however, are easily distinguished from *H. puta* males by the tibial apophysis.

Because of the differences in the males of the two groups, they are considered as separate species here. Further collections and field studies should elucidate the relationships of the populations concerned.

Distribution. Panama (Map 2).

Records. PANAMA. *Canal Zone.* Barro Colorado Island, numerous ♂♂♀♀ (A. M. Chickering); Madden Dam, 18 Aug. 1936, ♀, 25–31 July 1950, ♀ (A. M. Chickering); Summit, 7–10 July 1950, 4♀♀, 21–29 July 1950, 5♀♀, 16–17 Aug. 1950, 7♀♀:oo, 23–28 Aug. 1950, 4♀♀ (A. M. Chickering).

Hamataliwa cavata (Kraus)

Figures 17, 18, 29, 30, 73, 74, 109, 110. Map 2.

Oxyopeidon cavatum Kraus, 1955, Abh. Senckenb. Naturf. Ges., no. 493, p. 39, figs 99–101, ♂♀. Male holotype from San Salvador, El Salvador, in Senckenberg Museum, examined.

Measurements. Length of male holotype 4.3 mm, carapace width 1.8 mm, carapace length 2.3 mm.

Width of eye rows: AME .23 mm, ALE .78 mm, PLE 1.45 mm, PME 1.04 mm.

Segments of leg I: femur 2.4 mm, patella-tibia 3.0 mm, metatarsus 2.0 mm, tarsus 0.9 mm, total length 8.3 mm.

Length of patella-tibiae: II 2.8 mm, III 2.0 mm, IV 1.9 mm.

Length of female 6.0 mm, carapace width 2.3 mm, carapace length 2.6 mm.

Width of eye rows: AME .20 mm, ALE .62 mm, PLE 1.17 mm, PME .90 mm.

Segments of leg I: femur 2.5 mm, patella-tibia 3.2 mm, metatarsus 1.9 mm, tarsus 1.0 mm, total length I 8.6 mm.

Length of patella-tibiae: II 2.9 mm, III 2.0 mm, IV 2.0 mm.

Color. Male. Pattern illustrated in Figures 29 and 30. Face and chelicerae pale orange-yellow, lower edge of clypeus

lighter. Indistinct median white stripe from AME to lower edge of clypeus.

Carapace pale orange-yellow to golden.

Abdomen somewhat shriveled. Dorsum pale yellow, cardiac area with darker hairs overlying it. No well-defined darker markings. Venter of abdomen cream colored.

Legs pale yellow. Femora somewhat darker. No distinct darker markings.

Labium and endites pale yellow to cream. Outer margins of distal ends dark, heavily sclerotized. Sternum cream colored.

Color. Female. Pattern illustrated in Figures 17 and 18. Face and chelicerae light brownish orange. Darker at edges of face. Faint white stripe from ALE toward cheliceral condyles. Lighter median line from AME to lower edge of clypeus.

Carapace yellow-orange to golden, overlaid with brown spatulate hairs, abundant in eye region and at sides and posterior declivity.

Dorsum of abdomen yellow-orange to cream colored. Mixture of light hairs and brownish spatulate hairs. Mottled brown anteriorly with darker brown patches near posterior end as illustrated.

Legs yellow without darker markings.

Labium and endites pale yellow-orange. Sternum cream colored.

Diagnosis. Hamataliwa cavata is similar to *H. puta* in body structure, eye arrangement, and in the structure of the genitalia. Differences in bodily proportions between *H. cavata* and *H. puta* can be seen by comparing measurements.

The male palpi of the two species are very similar (compare Figs. 109 and 110 with Figs. 113–119), but the genitalia of the females are quite distinct (compare Figs. 73, 74 with Figs. 65–67). Because of the distinct epigynum and because of slight differences in palpal sclerites of the males, *H. cavata* is considered a separate species here.

Distribution. El Salvador (Map 2).

Record. EL SALVADOR, San Salvador, Tropical Institute, ♂ ♀ 700 m, 30 Apr. 1957 (A. Zilch).

Hamataliwa hista sp. n.

Figures 15, 16, 27, 28, 75, 76, 107, 108. Map 2.

Holotype. Male from Boquete, Panama, 4–11 Aug. 1954 (A. M. Chickering), in the Museum of Comparatize Zoology. The specific name is a noun in apposition meaning snake.

Measurements. Length of three males 4.7–5.1 mm, carapace width of four males 1.8–2.0 mm, carapace length 2.1–2.4 mm.

Width of eye rows: AME .23–.25 mm, ALE .67–.72 mm, PLE 1.22–1.34 mm, PME .84–.90 mm.

Segments of leg 1: femur 2.5 mm, patella-tibia 3.1–3.4 mm, metatarsus 2.1–2.3 mm, tarsus 1.0–1.1 mm, total length I 8.8–9.2 mm.

Length of patella-tibiae: II 2.8–3.0 mm, III 2.0–2.2 mm, IV 1.9–2.0 mm.

Length of ten females 5.8–7.4 mm, mean 6.49 mm; carapace width 2.0–2.2 mm, mean 2.15 mm; carapace length 2.5–2.7 mm, mean 2.60 mm.

Width of eye rows: AME .28–.30 mm, mean .292 mm; ALE .80–.85 mm, mean .827 mm; PLE 1.50–1.64 mm, mean 1.575 mm; PME 1.04–1.15 mm, mean 1.104 mm.

Segments of leg I: femur 2.5–2.8 mm, mean 2.59 mm; patella-tibia 3.1–3.5 mm, mean 3.33 mm; metatarsus 1.8–2.1 mm, mean 1.98 mm; tarsus .9–1.0 mm, mean .95 mm; total length 8.4–9.2 mm, mean 8.83 mm.

Length of patella-tibiae: II 2.7–3.1 mm, mean 2.96 mm; III 2.0–2.3 mm, mean 2.12 mm; IV 1.9–2.1 mm, mean 2.04 mm.

Color. Male. Pattern illustrated in Figures 27 and 28. Color essentially same as in female. Carapace yellow.

Cymbia of palpi brown. Labium, endites, and sternum somewhat lighter than in female.

Color. Female. Pattern illustrated in Figures 15 and 16. Face yellow-orange, lighter yellow along lower edge of clypeus. Chelicerae yellow-orange with sub-distal regions of basal segments lighter.

Carapace yellow-orange with scattered brown spatulate hairs along sides.

Dorsum of abdomen cream colored, overlaid with irregular patches of darker spatulate hair, denser in cardiac region and along sides. Venter cream to yellow.

Legs yellow without distinct markings. Distal segments darker.

Labium yellow to light brown. Endites yellow to brownish yellow. Sternum cream to pale yellow.

Diagnosis. Hamataliwa hista is similar to *H. puta* in eye arrangement and the structure of the male palpal organs (compare Figs. 107, 108 with Figs. 113–119). However, the cymbium is more oval and the embolus is longer in *H. hista.* The females are easily distinguished on the basis of the epigyna (compare Figs. 75, 76 with Figs. 65–67).

Distribution. Panama (Map 2).

Records. PANAMA. Boquete, 1–8 Aug. 1950, ♂:8♀♀, 4–11 Aug. 1954, 3♂♂:17♀♀ (A. M. Chickering).

Hamataliwa flebilis (O.P.-Cambridge)

Figures 13, 14, 25, 26, 70–72, 124, 125. Map 2.

Oxyopeidon flebile O. P. - Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:141, pl. 16, figs. 9, 9a–9c, ♀. Holotype male, designated by F.O.P.-Cambridge, from Bugaba, Panama, in British Museum (Natural History), examined. F.O.P. - Cambridge, 1902, *op. cit.,* 2:347, pl. 32, fig. 32, ♀.

Measurements. Length of male holotype 5.1 mm, carapace width 1.9 mm, carapace length 2.4 mm.

Width of eye rows: AME .27 mm, ALE .75 mm, PLE 1.37 mm, PME .97 mm.

Segments of leg I: femur 2.7 mm, patella-tibia 3.4 mm, metatarsus 2.3 mm, tarsus 1.0 mm, total length I 9.4 mm.

Length of patella-tibiae: II 3.0 mm, III 2.2 mm, IV 1.0 mm.

Length of ten females 5.7–7.4 mm, mean 6.46 mm; carapace width 1.9–2.3 mm, mean 2.09 mm; carapace length 2.3–2.7 mm, mean 2.50 mm.

Width of eye rows: AME .27–.30 mm, mean .294 mm; ALE .78–.86 mm, mean .837 mm; PLE 1.45–1.67 mm, mean 1.570 mm; PME 1.04–1.24 mm, mean 1.136 mm.

Segments of leg I: femur 2.4–2.9 mm, mean 2.53 mm; patella-tibia 2.8–3.4 mm, mean 3.15 mm; metatarsus 1.8–2.1 mm, mean 1.87 mm; tarsus .8–1.0 mm, mean .91 mm; total length I 8.2–9.3 mm, mean 8.45 mm.

Length of patella-tibiae: II 2.5–3.1 mm, mean 2.83 mm; III 1.9–2.4 mm, mean 2.07 mm; IV 1.8–2.2 mm, mean 1.96.

Color. Male. Pattern illustrated in Figures 25 and 26. Face and chelicerae yellow-orange, devoid of overlying hairs.

Carapace yellow-orange.

Dorsum of abdomen yellow, darker brownish along sides. Muscle depressions also marked by brownish hairs.

Venter of abdomen pale yellow.

Legs yellow. Labium and endites pale yellow. Sternum cream.

Palpi light yellow-orange with darker brown sclerites showing through cymbium.

Color. Female. Pattern illustrated in Figures 13 and 14. Face and chelicerae yellow-orange to orange-brown with fine clothing of white hair. Lighter yellowish along lower margin of clypeus and distal ends of chelicerae. The hexagonal area bounded by the eyes is reddish in some well-marked specimens.

Carapace yellow-orange to orange-brown with clothing of fine white hair. Several specimens have a clothing of fine brown hair rather than white.

Dorsum of abdomen cream to pale yellow. Cardiac area easily discernible, sometimes clothed with brown spatulate hairs. In most specimens there are only a few scattered brown hairs over much of the dorsal surface. They cover the cardiac region and form two spots posteriorly. In these forms a large patch of brown spatulate hairs occurs just posterior to the cervical groove.

Venter of abdomen cream to pale yellow without darker markings.

Proximal leg segments pale yellow without darker markings. Tarsi and metatarsi tend to be darker brownish yellow.

Labium, endites, and sternum cream to pale yellow.

Diagnosis. Hamataliwa flebilis is placed in the *puta* species group because of the greater width of the PME row as compared with the ALE (also compare measurements with *H. puta*) and because of the closeness of the AME to the ALE (Figs. 13, 14).

The palpal sclerites of *H. flebilis* are similar to those of other species in the *H. puta* complex, but the tibial apophysis is distinct from that of other members of this group (compare Figs. 124–125 with Figs. 107–119). The epigynum and internal genitalia of *H. flebilis* readily separate it from other females of this group (Figs. 70–72).

Records. MEXICO. *Chiapas.* Finca El Real, 1–7 July 1950, ♀ (C. M. Goodnight, L. Stannard).

COSTA RICA. San José, ♂ (E. Schmidt).

PANAMA. Bugaba (Chiriquí, 22 km NW of David), ♂:13♀♀ (G. C. Champion). *Canal Zone.* Barro Colorado Island, 20 July 1954, ♀o, 18 Aug. 1954, ♀, 4 Feb. 1958, ♀:3oo; Gamboa, 24 July 1950, ♀ (A. M. Chickering); Summit, 23 Apr. 1953 ♀♀ (A. M. Nadler). Chilibre, 11 July 1950, ♀ (A. M. Chickering).

Hamataliwa difficilis (O.P.-Cambridge)

Figures 40, 41, 85–88. Map 2.

Oxyopeidon difficile O. P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:142, pl. 16, figs. 13, 13a–13c, ♀. Female lectotype, here designated, from Amula, Guerrero, Mexico, in British Museum (Natural History), examined. F.O.P.-Cambridge, *op. cit.,* 2:348.

Oxyopeidon molestum O. P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:141, pl. 16, figs. 15, 15a–15c, ♀. Female holotype from Amula, Guerrero, Mexico, in British Museum (Natural History), examined. F.O.P.-Cambridge, 1902, *op. cit.,* 2:348, pl. 32, fig. 35, ♀. NEW SYNONYMY.

Discussion. Hamataliwa difficilis and *Hamataliwa molesta* described under *Oxyopeidon* by O. P.-Cambridge are undoubtedly the same species. (compare Figs. 85, 87 with Fig. 88). On examination, the holotype of *O. molestum* still retained a hard plug in the median depression of the epigynum. It is so drawn in figure 15c, plate 16 of the *Biologia Centrali-Americana, Arachnida, Araneidea,* volume I. Upon removal of this plug, the epigynum (Fig. 88) was found to be identical to that of *H. difficilis. Hamataliwa difficilis* was selected as the name of the species because of the more accurate drawing of the epigynum in figure 13c, plate 16 of the *Biologia.*

Measurements. Length of two females 5.2, 6.6 mm, carapace width 1.9, 1.9 mm, carapace length 2.2, 2.2 mm.

Width of eye rows (three females): AME .25, .27, .28 mm, ALE .70, .72, .77 mm, PLE 1.25, 1.34, 1.34 mm.

Segments of leg I: femur 2.4, 2.4, 2.5 mm; patella-tibia 2.8, 2.9, 3.1 mm; metatarsus 1.9, 1.9, 1.9 mm; tarsus .8, .9, 1.0 mm; total length I 7.8, 8.0, 8.4 mm.

Length of patella-tibiae: II 2.6, 2.7, 2.7 mm; III 2.0, 2.1, 2.1 mm; IV 1.9, 2.0, 2.0 mm.

Color. Female. Because of their condition, color descriptions of the above three specimens would serve no useful purpose. Instead, the original color descriptions of O. P.-Cambridge follow. They are both quoted because of the obvious differences in coloration.

Oxyopeidon molestum: "Cephalothorax and falces deep brown, thinly clothed with squamose grey hairs.

"The legs are pale yellowish, the femora of the first three pairs two-thirds brown at their anterior extremities, while that part of the femora of the fourth pair is marked with a more decided dark brown annulus, the tibiae also are dark brown at their anterior extremities.

"The abdomen is deep blackish-brown, with a pale patch at the fore extremity on

the upperside, bearing a short longitudinal black marking, this patch is conspicuous from numerous white hairs; two indistinct reddish round spots or blotches form a transverse line across the middle of the upperside. (The abdomen had evidently been more or less densely clothed with squamose and other hairs, of a grey, reddish, and yellowish colour, but many had been rubbed off.) The underside is nearly black, with a distinct yellowish border, and two nearly parallel longitudinal yellowish lines from the genital aperture, converging towards the hinder extremity."

Oxyopeidon difficile: "Cephalothorax yellow-brown, clothed with short grey hairs, the sides are marked with a broken marginal line and irregular converging lines of blackish hue.

"Legs brownish-yellow, an imperfect band across the middle of the femora, the posterior extremities of the tibiae blackish; the metatarsi of the third and fourth pair also indistinctly annulated with blackish.

"Abdomen yellowish-brown, clothed with short whitish and other hairs; the upperside has an irregular black bar along the middle, followed by some irregular black angular bars or chevrons above the spinners, and some irregular black patches or markings on the sides; the underside has a broad longitudinal dark brown band.

"The falces are yellow-brown, tolerably long, strong, clothed with short grey hairs.

"The maxillae, labium, and sternum are dull yellow, the maxillae and labium tinged with brown."

Diagnosis. Hamataliwa difficilis is associated with the *puta* species group. It is placed here chiefly because of the greater width of the PME as compared to the ALE (see measurements), and the position of the AME in relation to the AME (Figs. 40, 41).

The epigynum of *H. difficilis* is very distinct from that of all other species of *Hamataliwa* investigated (Figs. 85–88).

Distribution. Mexico (Map 2).

Record. MEXICO. *Guerrero.* Amula, 9.5 km NW of Chilapa, 3♀♀ (H. H. Smith).

Hamataliwa laeta (O.P.-Cambridge)

Figures 42, 79, 80. Map 2.

Oxyopeidon laetum O.P.-Cambridge 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:142, pl. 16, figs. 10, 10a–10c, ♀. Female holotype from Dos Caminos, Guerrero, Mexico, in British Museum (Natural History), examined. F.O.P.-Cambridge, 1902, *op. cit.*, 2:347, pl. 32, fig. 33, ♀.

Measurements. Length of female holotype 5.4 mm, carapace width 1.9 mm, carapace length 2.4 mm.

Width of eye rows: AME .27 mm, ALE .84 mm, PLE 1.47 mm, PME 1.14 mm.

Segments of leg I: femur 2.4 mm, patella-tibia 2.9 mm, metatarsus 1.7 mm, tarsus .9 mm, total length I 7.9 mm.

Length of patella-tibiae: II 2.6 mm, III 1.9 mm, IV 1.9 mm.

Color. Female holotype. Since the color has been altered by handling and long preservation in alcohol, the original description by O. P.-Cambridge is given.

"The cephalothorax is yellow-brown, the ocular area reddish; it is clothed with squamose grey hairs, of which one or more conspicuous lines mark out the ocular area and the limits of the clypeus.

"Falces similar in colour and clothing to the cephalothorax.

"Legs yellow, very slightly indeed tinged with brown near the middle of the femora.

"Abdomen dull brownish-yellow above, with two rather converging longitudinal black lines near the middle, and a distinct black patch on each side a little above the spinners, from which to a little way upwards is a series of short, indistinct, subangular, brownish lines or chevrons; there are also some other indistinct yellow-brown markings near the middle and on the sides. The abdomen is clothed with squamose grey hairs. The underside is dusky brown."

Diagnosis. The holotype female, al-

though mounted on a pin running through it longitudinally, is in relatively good condition. The structure of the epigynum together with the eye arrangement separates it from all other species of *Hamataliwa* studied. It is placed in the *puta* species group because of the greater width of the PME row compared with the ALE row (Fig. 42). The structure of the epigynum (Figs. 79, 80) is in general conformity with this group also, but until the male is discovered and the internal female genitalia studied, the placement of *H. laeta* in the *puta* species group remains an arbitrary decision.

Distribution. Mexico (Map 2).

Record. MEXICO. *Guerrero.* Dos Caminos, 37 km S of Chilpancingo, ♀ (H. H. Smith).

Hamataliwa crocata sp. n.

Figures 23, 24, 35, 36, 77, 78, 126, 127. Map 2.

Holotype. Male from Summit, Panama Canal Zone, 23–28 Aug. 1950 (A. M. Chickering), in Museum of Comparative Zoology. The specific name is an adjective meaning yellow.

Measurements. Length of four males 4.3–4.7 mm, carapace width 1.7–1.9 mm, carapace length 1.8–2.1 mm.

Width of eye rows: AME .23–.25 mm, ALE .70–.80 mm, PLE 1.30–1.48 mm, PME 1.00–1.13 mm.

Segments of leg I: femur 2.1–2.4 mm, patella-tibia 2.8–3.2 mm, metatarsus 1.9–2.1 mm, tarsus .9–1.0 mm, total length I 7.5–8.6 mm.

Length of patella-tibiae: II 2.5–2.9 mm, III 1.9–2.0 mm, IV 1.7–1.9 mm.

Length of 10 females 4.0–5.7 mm, mean 5.24 mm; carapace width 1.6–2.1 mm, mean 1.86 mm; carapace length 1.8–2.2 mm, mean 2.03 mm.

Width of eye rows: AME .25–.27 mm, mean .255 mm; ALE .78–.93 mm, mean .853 mm; PLE 1.40–1.73 mm, mean 1.573 mm; PME 1.08–1.38 mm, mean 1.230 mm.

Segments of leg I: femur 2.0–2.4 mm, mean 2.20 mm; patella-tibia 2.5–3.3 mm, mean 2.88 mm; metatarsus 1.5–1.9 mm, mean 1.67 mm; tarsus .8–.9 mm, mean .79 mm; total length I 6.7–8.4 mm, mean 7.53 mm.

Length of patella-tibiae: II 2.3–2.9 mm, mean 2.55 mm; III 1.6–2.0 mm, mean 1.84 mm; IV 1.5–2.0 mm, mean 1.76 mm.

Color. Male. Pattern illustrated in Figures 35 and 36. Coloration essentially as in the female except that the darker brown spatulate hairs are not as abundant. Cymbium of palpus dark brown.

Color. Female. Pattern illustrated in Figures 23 and 24. Face pale orange-yellow, beneath clothing of dark brown spatulate hairs. As the brown spatulate hairs are rubbed off the specimens become much paler in appearance. Chelicerae pale orange-yellow.

Carapace pale orange-yellow to brownish orange. Brown color contributed by spatulate hairs, thickest in eye region and along vertical sides.

Dorsum of abdomen cream to pale yellow, usually with clothing of closely packed dark brown hairs forming irregular pattern. Venter of abdomen cream color without darker median stripe.

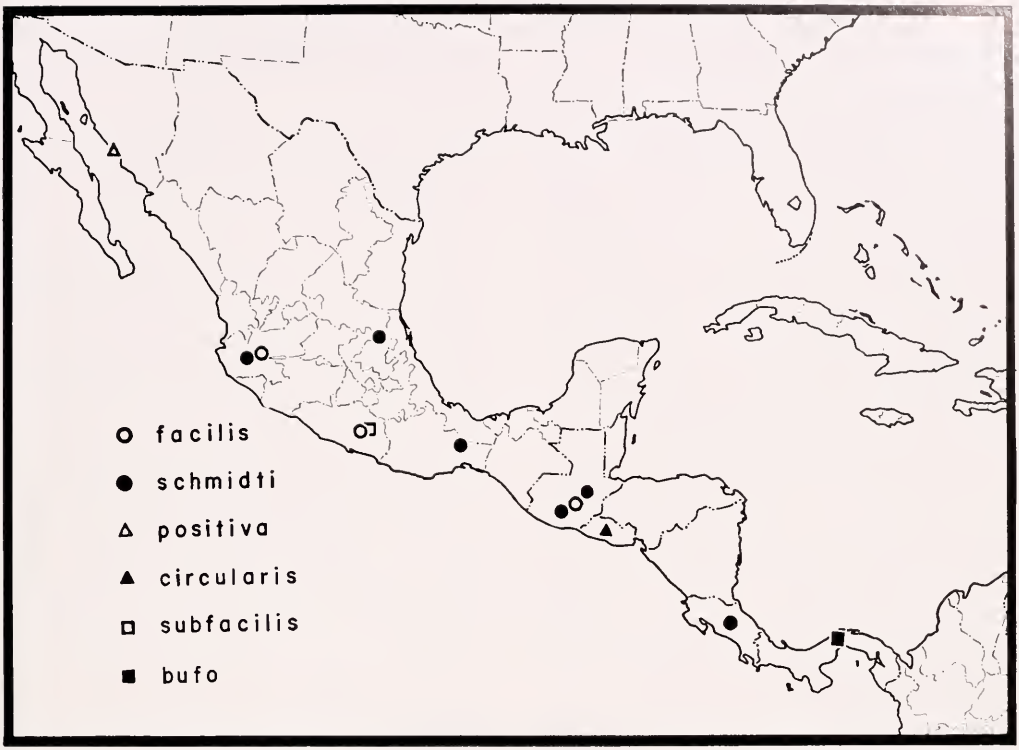
Legs pale yellow to yellow-orange, usually lighter than carapace.

Labium and endites cream to pale yellow. Sternum ivory to cream.

Diagnosis. Hamataliwa crocata is arbitrarily placed in the *puta* species group because of the width of the PME row in relation to the ALE (see measurements) and the position of the AME in relation to the ALE (Figs. 23, 24). Although the eye arrangement is reminiscent of *H. puta*, both the epigynum (Figs. 77, 78) and male palpus (Figs. 126, 127) of *H. crocata* are quite distinct from other members of the *puta* species group.

Distribution. Panama (Map 2).

Records. PANAMA. *Canal Zone.* Barro Colorado Island, 30 July 1950, ♀; Summit,



MAP 3

21–29 July 1950, ♂:8♀♀, 23–28 Aug. 1950, 4♂♂:♀ (A. M. Chickering).

Hamataliwa facilis (O.P.-Cambridge)

Figures 44, 94–98. Map 3.

Oxyopeidon facile O.P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1: 140, pl. 16, figs. 6, 6a–6c, ♀. Female holotype from Chilpancingo, Guerrero, Mexico, in British Museum (Natural History), examined.

Hamataliwa facilis F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:349, pl. 32, figs. 36, 36a, 36b, ♀.

Discussion. *Oxyopeidon facile* described by O. P.-Cambridge was placed in the genus *Hamataliwa* by F.O.P.-Cambridge because of the position of the AME in relation to the ALE. He also pointed out that the PME were farther apart than they were in other species of *Oxyopeidon*. The arrangement of the eyes in *H. facilis* (Fig. 44) is a distinctive feature of this species, but it is not considered a valid criterion for separating *H. facilis* generically from other species of *Oxyopeidon*, now also placed in *Hamataliwa*.

Measurements. Length of three females 6.8, 7.4, 7.9 mm; carapace width 2.4, 2.5, 2.6 mm; carapace length (estimated) 2.8, 3.0, 3.1 mm.

Width of eye rows: AME .30, .32, .33 mm; ALE 1.48, 1.48, 1.50 mm; PLE 2.29, 2.30, 2.30 mm; PME 1.84, 1.85, 1.88 mm.

Segments of leg I: femur 3.0, 3.0, 3.4 mm; patella-tibia 4.0, 4.1, 4.2 mm; metatarsus 2.2, 2.2, 2.4 mm, tarsus – –, 1.0 ,1.4 mm; total length – –, 10.2, 11.4 mm.

Length of patella-tibiae: II 3.5, 3.8, 4.0 mm; III 2.6, 2.8, 3.4 mm; IV 2.5, – –, – –, mm.

Color. Female. Pattern on face illustrated in Figure 44. Because the specimens representing this species are in poor condition and because discoloration is likely, the original description by O. P. Cambridge is given.

"Cephalothorax dark yellow, brown, clothed in parts (probably in a more perfect specimen entirely so) with white squamose hairs.

"Eyes on diffused black spots.

"Legs and palpi yellow-brown, paler than the cephalothorax.

"Falces similar in color to the cephalothorax, and clothed with white squamose hairs, especially towards the base.

"Maxillae, labium and sternum similar to the legs in colour.

"Abdomen dark brown on the upperside, clothed with short reddish and grey squamose hairs; along the middle of the fore part is a darker obscure stripe, and there are some black markings above the spinners; the sides have each a kind of obscure broken longitudinal stripe or line of patches and spots of yellow-brown, some of them more or less confluent, and appearing to be clothed with white hairs longer than the rest; these lines of spots end near the spinners. The underside has a broad, longitudinal, central, black-brown band, margined with a brownish-yellow stripe. The spinners are short, compact, and of a dark-brown colour."

Diagnosis. The female holotype of *H. facilis* has a unique epigynum as illustrated in Figures 94, 95. Although the epigyna of the two female paratypes are different (Figs. 96–98), the similarity of these two specimens to the holotype in other morphological features indicates conspecificity (compare measurements of the three specimens above). This particular case stresses the value of measuring a number of morphological components in order to determine the relationship between specimens. The epigyna of the paratypes somewhat resemble those of *H. positiva* or *H. schmidti* (compare Figs. 96–98 with Figs. 89–91, 93), but the eye arrangement of *H. facilis* readily separates it from these two species (compare Fig. 44 with Figs. 43, 46).

Distribution. Mexico, Guatemala (Map 3).

Records. MEXICO. *Jalisco.* ♀. *Guerrero.* Chilpancingo, ♀ (H. H. Smith).
GUATEMALA. ♀ (Sargent).

Hamataliwa positiva Chamberlin

Figures 43, 93. Map 3.

Hamataliwa positiva Chamberlin, 1924, Proc. California Acad. Sci., 12:677, fig. 118, ♀. Female holotype from San Carlos Bay, Sonora, July 7, 1921 (E. P. Van Duzee) in American Museum of Natural History (Calif. Acad. Sci. collection), examined.

Measurements. Length of female holotype 7.9 mm, carapace width 2.5 mm, carapace length 3.1 mm.

Width of eye rows: AME .33 mm, ALE 1.14 mm, PLE 1.97 mm, PME 1.65 mm.

Segments of leg I: femur 3.0 mm, patella-tibia 4.0 mm, metatarsus 2.3 mm, tarsus 1.1 mm, total length I 10.4 mm.

Length of patella-tibiae: II 3.7 mm, III 2.5 mm, IV 2.5 mm.

Color. Female. Pattern on face illustrated in Figure 43.

Integument of face and chelicerae, dark brown clothed with white appressed hair.

Carapace dark (chestnut) brown, heavily overlaid with white hair.

Dorsum of abdomen dark brown with overlying white hair. Venter with wide dark brown median stripe from epigastric furrow to spinnerets, enclosed by thick white appressed hair on each side.

Legs orange-brown, heavily fringed with white hairs.

Labium orange-brown, long white hair at base. Endites pale orange-brown, distal ends lighter, long white hair basally. Sternum orange-brown.

Diagnosis. Hamataliwa positiva resembles *H. unca* in size and eye arrangement and in the general shape of the epigynum. It is somewhat larger than *H. unca* and the legs are proportionally longer (compare measurements). The epigynum of *H. positiva* is greater in length from anterior to posterior than that of *H. unca.*

The epigyna of the paratypes of *H. facilis* resemble those of *H. positiva* (com-

pare Figs. 97, 98 with Fig. 93), but the eye arrangements in these two species are quite different (compare Fig. 44 with Fig. 43).

Distribution. Mexico (Map 3).

Records. MEXICO. *Sonora.* San Carlos Bay, 7 July 1921, ♀ (E. P. Van Duzee).

Hamataliwa unca Brady

Hamataliwa unca Brady, 1964, Bull. Mus. of Comp. Zool., 131:499, pls. 14–17, figs, 110, 111, 117, 118, 122, 123, 128, 129, ♂ ♀. Male holotype from Edinburg, Hidalgo Co., Texas, in American Museum of Natural History.

This species is recorded from the southern tip of Texas, and it almost certainly occurs further south into Mexico. The epigynum is somewhat similar to that of *H. positiva,* but it can be easily differentiated from the epigynum of that species. (compare figs. 117, 118 of Brady, 1964, with Fig. 93 of this paper). Also see the diagnosis of *H. positiva.*

Hamataliwa subfacilis (O.P.-Cambridge)

Figures 45, 92. Map 3.

Oxyopeidon subfacile O.P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, Araneidea, 1:141, pl. 16, figs. 5, 5a–5c, ♀. Female holotype from Amula, Guerrero, Mexico, in British Museum (Natural History), examined. F.O.P.-Cambridge, 1902, *op. cit.,* 2:348, pl. 32, figs. 34, 34a, ♀.

Discussion. In addition to the holotype, two other specimens were designated as "paratypes" in the British Museum collection. The epigyna of these two specimens are distinct from those of the holotype and after careful measurements of the carapace, eye rows, and legs, the specimens were placed in *H. schmidti.* They agree closely with *H. schmidti* in body size, eye arrangement, and leg length in addition to epigynal structure. *Hamataliwa subfacilis* has a uniquely shaped epigynum (Fig. 92) and it was first thought to be plugged by a tough matrix as it was in other specimens examined, but probing with a needle revealed the sclerotized region to be continuous. Therefore, the epigynum figured is a true representation as it appears in the holotype. It is still possible that the scalloped ventral rim may prove to be abnormal. Specimens having comparable bodily dimensions and agreeing in eye arrangement should be carefully checked against measurements of the holotype.

Measurements. Length of female holotype 8.0 mm, carapace width 2.9 mm, carapace length 3.6 mm.

Width of eye rows: AME .35 mm, ALE 1.10 mm, PLE 2.05 mm, PME 1.50 mm.

Segments of leg I: femur 3.5 mm, patella-tibia 4.4 mm, metatarsus 2.5 mm, tarsus 1.2 mm, total length I 11.6 mm.

Length of patella-tibiae: II 4.0 mm, III 3.0 mm, IV 2.9 mm.

Color. Female. Pattern on face illustrated in Figure 45. Following is the original description by O.P.-Cambridge:

"The general colours are very much like those of *O. facile,* but the femora and the base of the tibiae are marked with a not very distinct, dark brown annulus; the general hue of the legs is brownish-yellow, that of the cephalothorax and falces yellow-brown, darker than the legs. The abdomen on the sides and upper part is, in front, of a dull luteous-yellow colour, dark brown behind towards the sides, with a central longitudinal dentated stripe of brown on the fore half, followed towards the spinners by a series of dark brown angular lines or chevrons; the underside has a broad, longitudinal, central dark brown band. The abdomen, like that of *O. facile,* appears to have been more or less covered with squamose grey and other hairs, most of which have been rubbed off."

The holotype is darker in color than it is in the above description. The face, chelicerae, and carapace are reddish brown and the abdomen is tan or beige in color. This color change may be the result of many years in preservative.

Diagnosis. Hamataliwa subfacilis is similar to *H. schmidti* in body size, eye ar-

rangement, and leg length. However, the ratio of AME width to ALE width is different (see measurements) in the two species and the eyes seem to occupy a proportionally larger area of the carapace in *H. schmidti* than they do in *H. subfacilis*. In addition the epigynum of *H. subfacilis* is unique in shape (compare Fig. 92 with Figs. 89–91).

Distribution. Mexico (Map 3).

Records. MEXICO. *Guerrero.* Amula, 9.5 km NW of Chilapa, ♀ (H. H. Smith).

Hamataliwa schmidti Reimoser

Figures 46, 47, 89–91. Map 3.

Hamataliwa schmidti Reimoser, 1939, Ann. Natur. Mus. Wein, 50:342–343, fig. 5, ♀. Two female syntypes from San José, Costa Rica, in Natural History Museum, Vienna, examined.

Measurements. Length of nine females 6.2–9.2 mm, mean 7.84 mm; carapace width 2.4–2.9 mm, mean 2.65 mm; carapace length 2.7–3.6 mm, mean 3.05 mm.

Width of eye rows: AME .30–.40 mm, mean .347 mm; ALE 1.03–1.45 mm, mean 1.233 mm; PLE 1.80–2.43 mm, mean 2.114 mm; PME 1.38–1.93 mm, mean 1.619 mm.

Segments of leg I: femur 2.4–3.7 mm, mean 3.16 mm; patella-tibia 3.8–5.0 mm, mean 4.17 mm; metatarsus 2.1–2.7 mm, mean 2.33 mm; tarsus 1.0–1.4 mm, mean 1.11 mm; total length I 9.8–12.7 mm, mean 10.77 mm.

Length of patella-tibiae: II 3.3–4.5 mm, mean 3.75 mm; III 2.5–3.3 mm, mean 2.75 mm; IV 2.4–3.2 mm, mean 2.64 mm.

Color. Female. Pattern illustrated in Figures 46 and 47.

Face and chelicerae yellow-orange to reddish brown, lighter yellowish along lower edge of clypeus. Long white hair along lateral margins of face and over front of chelicerae.

Carapace yellow-orange to reddish brown, covered with intermixture of white and dark brown hair.

Dorsum of abdomen pale yellow to cream ground color with irregular pattern of bands and spots formed by brown and white spatulate-shaped, appressed hairs that impart an over-all light brown or gray appearance. Cardiac area often darkly accented as in specimen figured. Venter of abdomen with broad median brown stripe from epigastric furrow to base of spinnerets. The stripe outlined by thinner areas of white laterally.

Legs yellow to yellow-orange, fringed with long white hair along prolateral and retrolateral margins.

Labium and endites pale yellow to light yellow-orange, distal ends ivory. Sternum ivory to pale yellow.

Diagnosis. The specimens classified as *H. schmidti* show considerable diversity in size. They all agree in the structure of the epigynum, eye arrangement, and body proportions. This species is of relatively wide occurrence in the Mexican and Central American region and the size differences may be simply a reflection of the geographic variability of widely separated specimens. There is less likelihood, I think, that more than one species is represented in this assortment. Additional specimens and particularly males associated with females should clarify the picture.

Hamataliwa schmidti resembles *H. subfacilis* in body size, eye arrangement, and leg length, but the epigyna of these two species are quite distinct (compare Figs. 89, 91 with Fig. 92). The shape of the epigynum in *H. positiva* is similar to that of *H. schmidti*, but the genitalia of the latter are much larger in size (compare Figs. 89–91 with Fig. 93).

Hamataliwa schmidti resembles *H. grisea* and *H. facilis* in size and general appearance, and there are similarities in eye arrangement and the structure of the genitalia in these three species. The three species can be separated by measurements of the eye rows and genitalic characteristics (compare Figs. 89–91 with Figs. 94–98 of this paper and figs. 115, 116 of Brady, 1964).

Distribution. Mexico to Costa Rica (Map 3).

Records. MEXICO. *San Luis Potosí.* Tamazunchale, 20 May 1952, ♀ (Cazier, Gertsch, Schrammel). *Jalisco.* ♀. *Oaxaca.* Tolosa, 1–12 Apr. 1947, ♀ (B. Malkin).

GUATEMALA. ♀♀ (F. Sargent) Capetillo, 20–23 Aug. 1947, ♀, San Jeronimo, 24–26 July 1947, ♀ (C., P. Vauric).

COSTA RICA. La Caja near San José, 1932, 3♀♀ (E. Schmidt).

Hamataliwa grisea Keyserling

Hamataliwa grisea Keyserling, 1887, Verh. Zool. -Bot. Wien, 37:458, pl. 6, fig. 24, ♀. Female holotype from North America, in the British Museum (Natural History), examined.

Hamataliwa grisea: Simon, 1898, Histoire naturelle des Araignées, 2(2):375, 377, 378, 380, figs. 373, 379. Comstock, 1912, The Spider Book, p. 660; *op. cit.*, rev. ed., 1940, p. 668.

Hamataliwa grisea is the most common species of this genus found in North America. Its range extends from the southern United States southward into Guanajuato and Jalisco (see map 5 of Brady, 1964).

Of the species considered in this paper, *H. grisea* is closest to *H. schmidti* and *H. facilis* in size and general morphology. *Hamataliwa grisea* is differentiated from both of these species by eye arrangement (compare measurements) and the structure of the genitalia (compare figs. 115, 116 of Brady, 1964, with Figs. 89–91, 94, 95 of this paper). For a discussion of the natural history of this species see Brady, 1964, p. 503.

Hamataliwa circularis (Kraus)

Figures 37, 38, 99, 100. Map 3.

Oxyopeidon circularis Kraus, 1955, Abh. Senckenb. Naturf. Ges., 493:39, pl. 5, fig. 98, ♀. Female holotype from 6 km N of Los Blancos, El Salvador, in Senckenberg Museum, examined.

Measurements. Length of female holotype 6.3 mm, carapace width 1.8 mm, carapace length 2.1 mm.

Width of eye rows: AME .27 mm, ALE .72 mm, PLE 1.29 mm, PME 1.00 mm.

Segments of leg 1: femur 1.9 mm, patella-tibia 2.3 mm, metatarsus 1.5 mm, tarsus 0.7 mm, total length I 6.4 mm.

Length of patella-tibiae: II 2.1 mm, III 1.9 mm, IV 1.8 mm.

Color. Female. Pattern illustrated in Figures 37 and 38. Face and chelicerae yellow-orange overlaid with gray. Lower edge of clypeus and distal ends of chelicerae yellowish.

Carapace yellow-orange overlaid with gray, giving this region a darker orange or reddish brown appearance.

Dorsum of abdomen pale yellow or cream colored with gray overtones. Venter of abdomen cream with longitudinal black inclusions beneath integument.

Legs yellow with distal segments light orange-brown.

Labium, endites, and sternum cream.

Diagnosis. The eye arrangement of this species is reminiscent of certain species of *Oxyopes*, but the relative length of the legs (I-II-III-IV) and the epigynum are characteristic of *Hamataliwa.*

Hamataliwa circularis is closest to members of the *puta* species group in having the PME row wider than the ALE row. However, the epigynum of *H. circularis* is distinct, with the seminal receptacles widely separated (Figs. 99, 100); this feature was not found in any of the other species of *Hamataliwa* in this investigation. The structure of the male palpus will determine whether or not this species should be placed in the *puta* group.

Distribution. El Salvador (Map 3).

Records. EL SALVADOR. Forest 6 km N. of Los Blancos, 24 Apr. 1951, ♂ San Salvador, Tropical Institute, 700 m, 30 Apr. 1950, ♀, Sept. 1951, ♀ (A. Zilch).

Hamataliwa bufo sp. n.

Figures 48, 49, 101–103. Map 3.

Holotype. Female from Barro Colorado Island, Panama Canal Zone, 1–4 July 1950 (A. M. Chickering), in Museum of Comparative Zoology.

Measurements. Length of four females 6.1–7.7 mm, carapace width 2.4–2.6 mm, carapace length 2.9–3.2 mm.

Width of eye rows: AME .32–.33 mm, ALE .84–.90 mm, PLE 1.59–1.69, PME .95–1.04 mm.

Segments of leg I: femur 2.4–2.6 mm, patella-tibia 2.9–3.2 mm, metatarsus 1.9–2.0 mm, tarsus 1.0 mm, total length I 8.3–8.8 mm.

Patella-tibiae: II 2.8–3.1 mm, III 2.1–2.3 mm, IV 2.0–2.2 mm.

Color. Pattern illustrated in Figures 48 and 49. Face and chelicerae brown with heavy clothing of white, appressed hair, lower edge of clypeus protuberant, yellowish. Tufts of white hair above PLE and prominent tufts at dorsum of carapace between PME (see Fig. 48).

Carapace brown with thick clothing of intermixed white and dark brown hair forming an irregular pattern. Heavy fringes of white hair along lower edge of cephalothorax in one specimen.

Dorsum of abdomen mottled gray in appearance due to mixture of white and black hair. Venter with median area gray-brown from epigastric furrow to spinnerets, outlined in pale yellow or cream. Pale yellow or cream anterior to epigastric furrow.

Legs yellow-brown to brown with ventral surface lighter yellowish.

Labium and endites yellow to brownish yellow with distal ends ivory. Sternum yellow.

Diagnosis. Hamataliwa bufo is readily distinguished from other species of *Hamataliwa* by its extremely high cephalothorax, and its squat, robust short-legged appearance. In addition the clypeus is very high and protuberant along its lower edge, with the anterior face of the chelicerae flat and not rounded as in other species of the genus.

Distribution. Panama (Map 3).

Records. PANAMA. *Canal Zone.* Barro Colorado Island, 3–5 July 1936, ♀, 1–4 July 1950, ♀; Chilibre, 8 July 1950, ♀; Fort Sherman 14–16 Aug. 1939, ♀ (A. M. Chickering).

MAP 4

Hamataliwa tricuspidata (F.O.P.-Cambridge)

Figures 50–53, 104–106, 128, 129. Map 4.

Oxyopes tricuspidatus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:343, pl. 32, figs. 17, 17a–17b, ♂. Male holotype from Bugaba, Panama, in British Museum (Natural History), examined.

Oxyopes clypeatus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:345, pl. 32, fig. 26, ♀. Female holotype from Bugaba, Panama, in British Museum (Natural History), examined. NEW SYNONYMY.

Measurements. Length of eight males 5.0–5.8 mm, mean 5.34 mm; carapace width 1.9–2.2 mm, mean 1.99 mm; carapace length 2.3–2.6 mm, mean 2.43 mm.

Width of eye rows: AME .28–.30 mm, mean 2.94 mm; ALE .58–.68 mm, mean .628 mm; PLE 1.05–1.15 mm, mean 1.106 mm; PME .58–.63 mm, mean .600 mm.

Segments of leg I: femur 2.3–2.7 mm, mean 2.48 mm; patella-tibia 2.9–3.4 mm, mean 3.04 mm; metatarsus 2.0–2.5 mm, mean 2.27 mm; tarsus .9–1.1 mm, mean .98 mm; total length I 8.2–9.6 mm, mean 8.78 mm.

Patella-tibiae: II 2.6–3.2 mm, mean 2.84 mm; III 2.0–2.4 mm, mean 2.11 mm; IV 2.0–2.4 mm, mean 2.11 mm.

Length of eight females 6.3–8.8 mm, mean 7.39 mm; carapace width 2.2–2.5 mm, mean 2.34 mm; carapace length 2.7–3.3 mm, mean 3.01 mm.

Width of eye rows: AME .33–.38 mm, mean .341 mm; ALE .73–.75 mm, mean .731 mm; PLE 1.28–1.43 mm, mean 1.319 mm; PME .68–.73 mm, mean .706 mm.

Segments of leg I: femur 2.5–3.0 mm, mean 2.78 mm; patella-tibia 3.0–3.7 mm, mean 3.28 mm; metatarsus 2.1–2.6 mm, mean 2.34 mm; tarsus .9–1.1 mm, mean 1.03 mm; total length I 8.6–10.3 mm, mean 9.42 mm.

Patella-tibiae: II 2.8–3.5 mm, mean 3.13 mm; III 2.0–2.7 mm, mean 2.37 mm; IV 2.1–2.8 mm, mean 2.44 mm.

Color. Male. Pattern illustrated in Figures 52 and 53. Face pale yellow to yellow-orange, darker vertical stripes from ALE to edge of clypeus. Median area of lower edge of clypeus cream.

Carapace yellow-orange, darker brownish along vertical sides. Light scale-like hairs contribute iridescent sheen, predominant laterally and at posterior declivity.

Dorsum of abdomen cream to brownish yellow, with dark brown indentations about one-third distance from spinnerets to base, accented by white spots. Sides of abdomen brown. Median area of venter brown, enclosed by narrow yellow stripes laterally.

Legs yellow-orange. Darker, brownish on ventral surface of femora. Legs covered with appressed spatulate hairs that give iridescent sheen.

Labium and endites yellow to yellow-orange with distal ends ivory. Sternum yellow.

Cymbia of palpi black.

Color. Female. Pattern illustrated in Figures 50 and 51. Face pale yellow to orange-yellow with darker, yellow-brown stripes from ALE to lower edge of clypeus and continuing to distal end of chelicerae. Median area of clypeus cream colored.

Carapace pale orange-yellow. Sides with brown spatulate hairs.

Dorsum of abdomen cream to pale yellow. Dark brown indentations one-third distance from spinnerets to base. Venter cream colored with faint brownish median stripe.

Legs yellow with scattered dusky hairs. Ventral surface of femora brownish yellow.

Labium, endites, and sternum yellow. Endites often with brownish overtones.

Diagnosis. Hamataliwa tricuspidata is very different from other species of *Hamataliwa* considered in this paper. The color pattern, eye arrangement, and long tapering abdomen are reminiscent of some species of *Oxyopes*. However, the relative length of the legs and genitalic characteristics place it close to *Hamataliwa*.

Although the order of leg length in this species is I-II-IV-III (with I longest), patella-tibia IV is only slightly longer than patella-tibia III. In this respect *H. tricuspidata* is closest to *Hamataliwa* since in *Oxyopes* species examined, patella-tibia IV is much longer than patella-tibia III as shown in Table II, page 493 (Brady, 1964). Correlated with this is the fact that leg IV in *Oxyopes* species is much more developed than it is in *Hamataliwa* species, and this development is related to the habits of these spiders.

At this stage it would appear that *H. tricuspidata* is intermediate between *Oxyopes* and *Hamataliwa*, having some characters in common with the former and others with the latter.

The female genitalia (Figs. 104–106) and the male palpus (Figs. 128, 129) of *H. tricuspidata* resemble those of other species of *Hamataliwa* and that resemblance is considered the most important factor here. An alternative to placing *H. tricuspidata* in *Hamataliwa* would be to establish a new genus for this species, but until much more is known of the Neotropical oxyopids the more conservative path seems the best.

Distribution. Costa Rica, Panama, and southeastward to British Guiana (Map 4).

Records. COSTA RICA. San José, ♂♀ (N. Banks).

PANAMA. ♀♀ (N. Banks). Arraiján, 6–9 July 1950, ♂♂♀o (A. M. Chickering). Bugaba (Chiriquí, 22 km NW of David), ♀♀ (G. C. Champion). *Canal Zone.* Barro Colorado Island, 16 June–15 July 1935, ♀;

Madden Dam, 27 July 1954, ♂. Chilibre, 8 July 1950, ♂ (A. M. Chickering).

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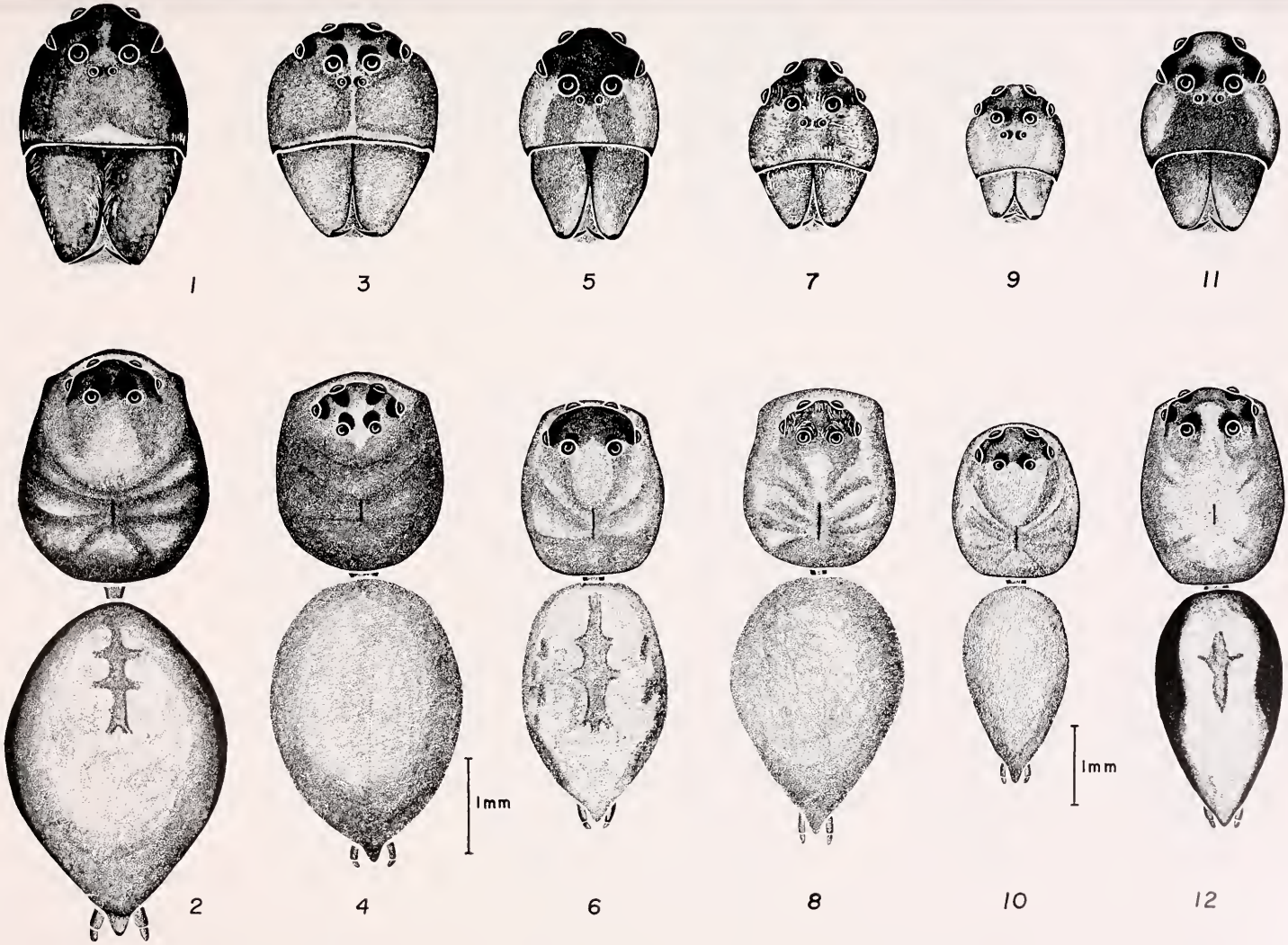
INDEX

Valid names are printed in italics.
Page numbers refer to main references.

absolutum 78
absolutum obliquum 78
annulipes 82
banksi 82
barroana 85
brevis 82
brunnea 83
bufo 99
cambridgei 82
cavata 89
cheta 86
circularis 99
clypeatus 100
crocata 94
difficilis 92
facilis 95
flebilis 91
globosa 86
grisea 99
helia 83
hista 90
laeta 93
molestum 92
positiva 96
puta 87
schmidti 98
subfacilis 97
triangularis 84
tricuspidata 100
tristani 78
unca 97
ursa 88

Figs. 1–2. *Hamataliwa cheta* sp. n., female from Cobán, Guatemala, July 1947. 1. Face view. 2. Dorsal view.
Figs. 3–4. *Hamataliwa banksi* Mello-Leitão, female lectotype from Cerro del Taste, Territorio Sur, Baja California. 3. Face view. 4. Dorsal view.
Figs. 5–6. *Hamataliwa barroana* (Chamberlin), female from Barro Colorodo Island, Panama Canal Zone, 4 July 1954. 5. Face view. 6. Dorsal view.
Figs. 7–8. *Hamataliwa triangularis* (Kraus), female from Barro Colorado Island, Panama Canal Zone, 23–30 June 1939. 7. Face view. 8. Dorsal view.
Figs. 9–10. *Hamataliwa triangularis* (Kraus), male from Barro Colorado Island, Panama Canal Zone, 23–30 June 1939. 9. Face view. 10. Dorsal view.
Figs. 11–12. *Hamataliwa globasa* (F.O.P.-Cambridge), from Tamazunchale, San Luis Potosí, 20 May 1952. 11. Face view. 12. Dorsal view.
Scale on the left is for Fig. 4 and *all* face views. Scale on the right is for all dorsal views except Fig. 4.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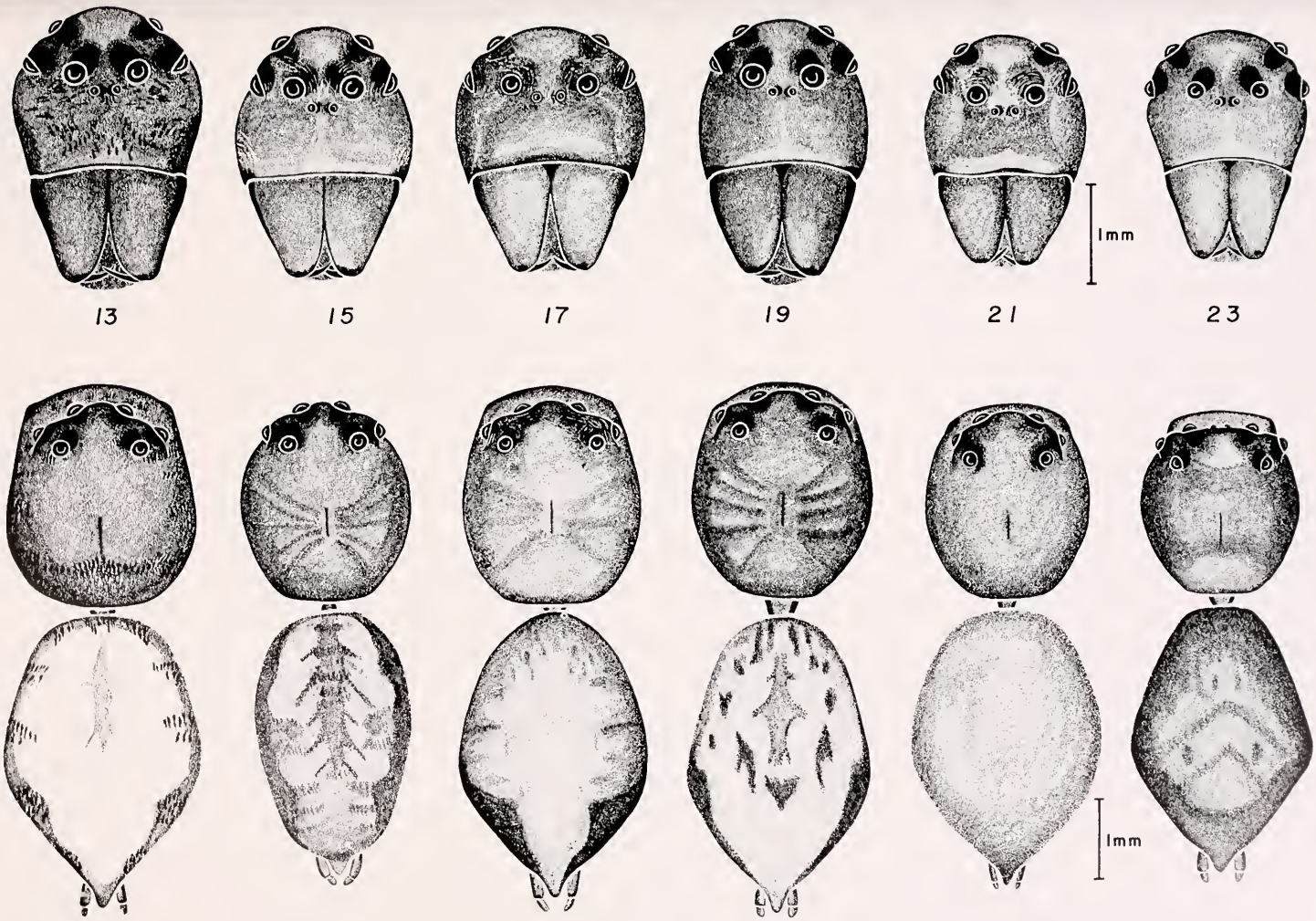
Figs. 13–14. *Hamataliwa flebilis* (O.P.-Cambridge), female from Gamboa, Panama, 24 July 1954. 13. Face view. 14. Dorsal view.
Figs. 15–16. *Hamataliwa hista* sp. n., female from Boquete, Panama, 4–11 Aug. 1954. 15. Face view. 16. Dorsal view.
Figs. 17–18. *Hamataliwa cavata* (Kraus), female from San Salvador, El Salvador, 30 Apr. 1951. 17. Face view. 18. Dorsal view.
Figs. 19–20. *Hamataliwa ursa* sp. n., female allotype from Barro Colorado Island, Panama Canal Zone, 1–4 July 1950. 19. Face view. 20. Dorsal view.
Figs. 21–22. *Hamataliwa puta* (O.P.-Cambridge), female allotype from Bugaba, Panama. 21. Face view. 22. Dorsal view.
Figs. 23–24. *Hamataliwa crocata* sp. n., female from Barro Colorado Island, Panama Canal Zone, 21–29 July 1950. 23. Face view. 24. Dorsal view.
Lower scale is for dorsal views. Upper scale is for face views.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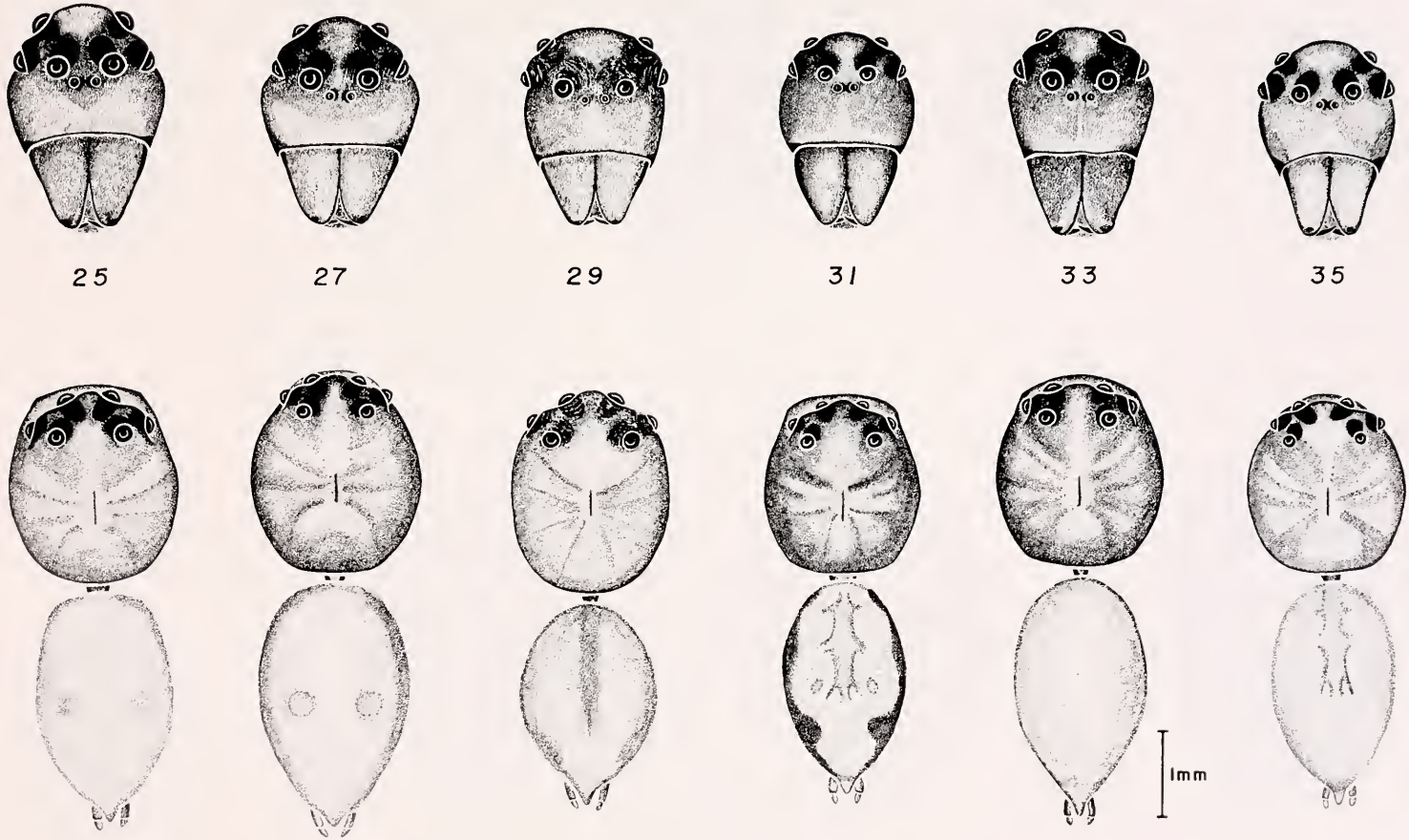
Figs. 25–26. *Hamataliwa flebilis* (O.P.-Cambridge), male holotype from Bugaba, Panama. 25. Face view. 26. Dorsal view.
Figs. 27–28. *Hamataliwa hista* sp. n., male holotype from Boquete, Panama, 4–11 Aug. 1954. 27. Face view. 28. Dorsal view.
Figs. 29–30. *Hamataliwa cavata* (Kraus), male holotype from San Salvador, El Salvador, Nov. 1951. 29. Face view. 30. Dorsal view.
Figs. 31–32. *Hamataliwa ursa* sp. n., male holotype from Barro Colorado Island, Panama Canal Zone, June 1950. 31. Face view. 32. Dorsal view.
Figs. 33–34. *Hamataliwa puta* (O.P.-Cambridge), male lectotype from Bugaba, Panama. 33. Face view. 34. Dorsal view.
Figs. 35–36. *Hamataliwa crocata* sp. n., male holotype from Summit, Panama Canal Zone, 23–28 Aug. 1950. 35. Face view. 36. Dorsal view.
Scale is for dorsal views.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Figs. 37–38. *Hamataliwa circularis* (Kraus), female holotype from 6 km N of Los Blancos, El Salvador, 24 Apr. 1951. 37. Face view. 38. Dorsal view.

Fig. 39. *Hamataliwa brunnea* (F.O.P.-Cambridge), face view of female holotype from Atoyac, Veracruz.

Figs. 40–41. *Hamataliwa difficilis* (O.P.-Cambridge), Amula, Guerrero. 40. Face view of female paratype. 41. Face view of female holotype of *Oxyopeidan molestum* (O.P.-Cambridge) = *Hamataliwa difficilis*.

Fig. 42. *Hamataliwa laeta* (O.P.-Cambridge), face view of female holotype from Dos Caminos, Guerrero.

Fig. 43. *Hamataliwa positiva* Chamberlin, face view of female holotype from San Carlos Bay, Sonora, 7 July 1921.

Fig. 44. *Hamataliwa facilis* (O.P.-Cambridge), face view of female holotype from Chilpancingo, Guerrero.

Fig. 45. *Hamataliwa subfacilis* (O.P.-Cambridge), face view of female holotype from Amula, Guerrero.

Scale on the left is for Fig. 38. Scale on the right is for face views.

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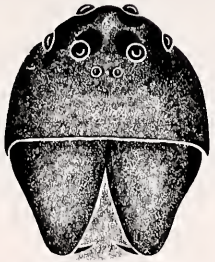

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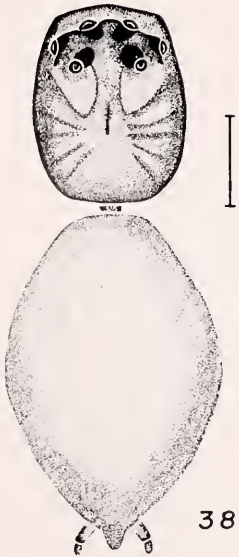

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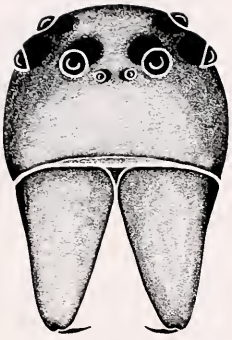
Figs. 46–47. *Hamataliwa schmidti* Reimoser, female syntype from San José, Costa Rica. 46. Face view. 47. Dorsal view.
Figs. 48–49. *Hamataliwa bufo* sp. n., female holotype from Barro Colorado Island, Panama Canal Zone, 1–4 July 1950. 48. Face view. 49. Dorsal view.
Figs. 50–53. *Hamataliwa tricuspidata* (F.O.P.-Cambridge), from Arraijan, Panama, 6–9 July 1950. 50. Face view of female. 51. Dorsal view of female. 52. Face view of male. 53. Dorsal view of male.



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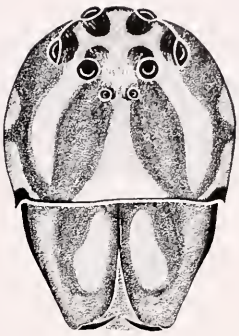

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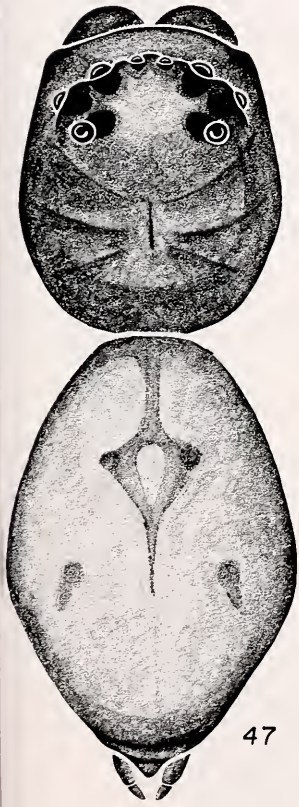

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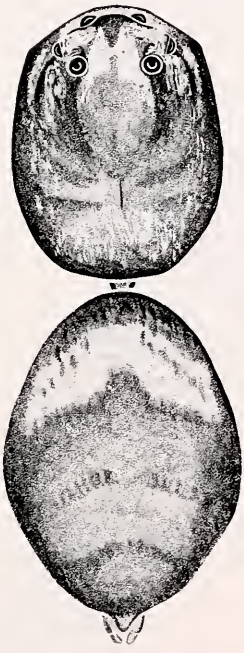

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Figs. 54–57. *Hamataliwa banksi* (Mello-Leitão), females from Cerra del Taste, Territorio Sur, Baja California. 54. Epigynum of paralectotype. 55. Internal genitalia of paralectotype. 56–57. Epigynum of lectotype drawn from different angles.

Fig. 58. *Oxyopes annulipes* F.O.P.-Cambridge = *Hamataliwa banksi* (Mello-Leitão), epigynum of holotype from Amula, Guerrero.

Fig. 59. *Hamataliwa brunnea* (F.O.P.-Cambridge), epigynum of female holotype from Atoyac, Veracruz.

Fig. 60. *Hamataliwa barroana* (Chamberlin), internal genitalia of female from Barro Colorado Island, Panama Canal Zone, 4 July 1954.

Fig. 61. *Hamataliwa barroana* (Chamberlin and Ivie), epigynum of female holotype from Barro Colorado Island, Panama Canal Zone, Aug. 1928.

Fig. 62. *Hamataliwa barraana* (Chamberlin), epigynum of female from Barro Colorado, Panama Canal Zone, 4 July 1954.

Figs. 63–64. *Hamataliwa cheta* sp. n., female from Cobán, Guatemala, July 1947. 63. Internal genitalia. 64. Epigynum. Scale is for all figures of epigyna.

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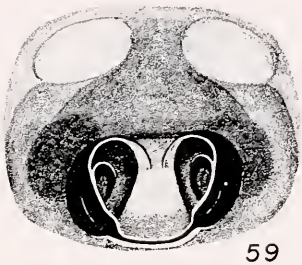

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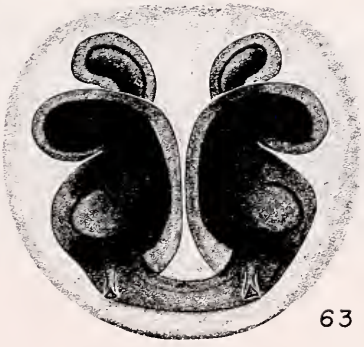

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Figs. 65–67. *Hamataliwa puta* (O.P.-Cambridge), female paratypes from Bugaba, Panama. 65. Internal genitalia. 66. Epigynum. 67. Epigynum of "allotype."

Figs. 68–69. *Hamataliwa ursa* sp. n., female from Barro Colorado Island, Panama Canal Zone, 1–4 July 1950. 68. Internal genitalia. 69. Epigynum.

Figs. 70–72. *Hamataliwa flebilis* (O.P.-Cambridge), female paratypes from Bugaba, Panama. 70. Epigynum of "allotype." 71. Epigynum. 72. Internal genitalia.

Figs. 73–74. *Hamataliwa cavata* (Kraus), female allotype from San Salvador, El Salvador, 30 Apr. 1951, epigynum mounted in glycerine gel. 73. Dorsal view. 74. Ventral view.

Figs. 75–76. *Hamataliwa hista* sp. n., female from Boquete, Panama, 4–11 Aug. 1954. 75. Internal genitalia. 76. Epigynum.

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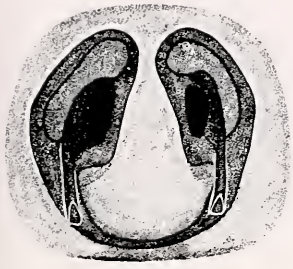

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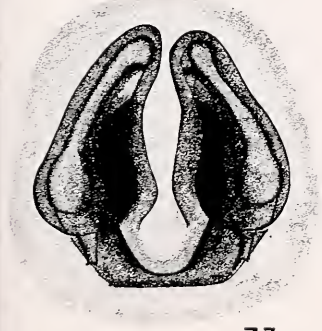

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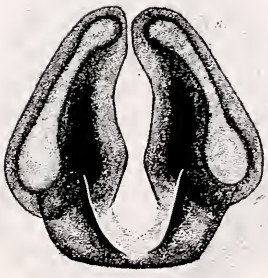

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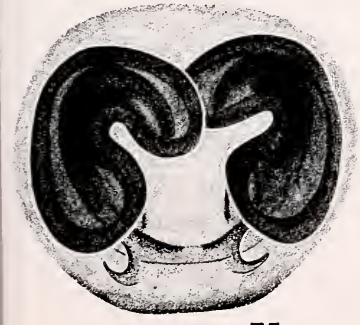

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Figs. 77–78. *Hamataliwa cracata* sp. n., female from Summit, Panama Canal Zone, 21–29 July 1950. 77. Internal genitalia. 78. Epigynum.

Figs. 79–80. *Hamataliwa laeta* (O.P.-Cambridge), female holotype from Das Caminos, Guerrera. 79. Epigynum, drawn Mar. 1968. 80. Epigynum, drawn June 1963.

Figs. 81–82. *Hamataliwa triangularis* (Kraus), female from Barro Colorado Island, Panama Canal Zone, 23–30 June 1939. 81. Internal genitalia. 82. Epigynum.

Fig. 83. *Hamataliwa triangularis* (Kraus), epigynum of female holotype from San Salvador, El Salvador, 21 June 1961, mounted in glycerine gel.

Fig. 84. *Oxyopes globosus* F.O.P.-Cambridge = *Hamataliwa triangularis* (Kraus), epigynum of female paratype from Bugaba, Panama.

Figs. 85–88. *Hamataliwa difficilis* (O.P.-Cambridge), females from Amula, Guerrera. 85. Epigynum of lectotype. 86. Internal genitalia of paralectotype. 87. Epigynum of paralectotype. 88. Epigynum of holotype of *Oxyopeidan malestum* O.P.-Cambridge = *Hamataliwa difficilis*.

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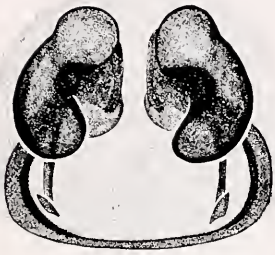

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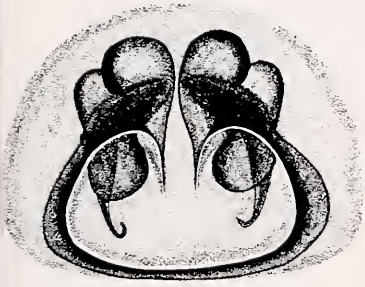

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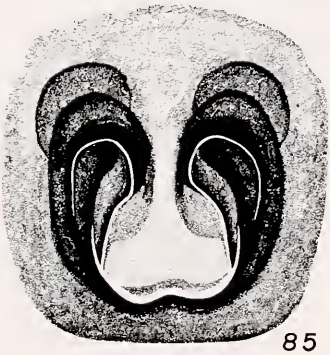

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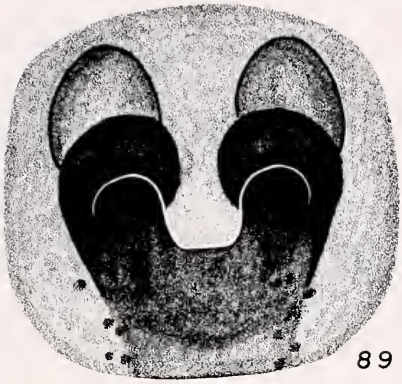
Fig. 89. *Homotoliwa schmidti* Reimoser, epigynum of female from Guatemala.
Figs. 90–91. *Homotoliwa schmidti* Reimoser, female syntype from San José, Costa Rica. 90. Internal genitalia. 91. Epigynum.
Fig. 92. *Homataliwa subfacilis* (O.P.-Cambridge), epigynum of female holotype from Amula, Guerrero.
Fig. 93. *Homotoliwa positiva* Chamberlin, epigynum of female holotype from San Carlos Bay, Sonora, 7 July 1921.
Figs. 94–95. *Homataliwa facilis* (O.P.-Cambridge), female holotype from Chilpancingo, Guerrero. 94. Epigynum drawn April 1968. 95. Epigynum drawn June 1963.
Figs. 96–98. *Homotoliwa facilis* (O.P.-Cambridge), female paratypes from Chilpancingo, Guerrero. 96. Internol genitalia. 97. Epigynum. 98. Epigynum.



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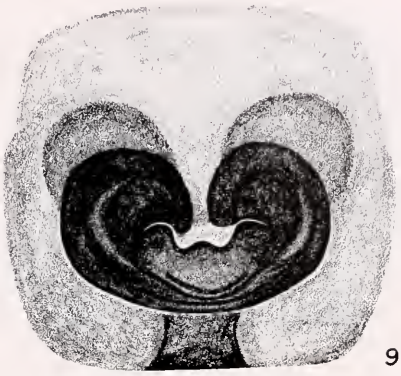

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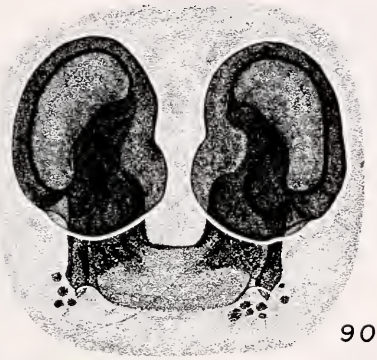

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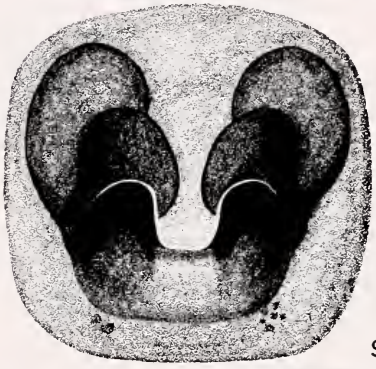

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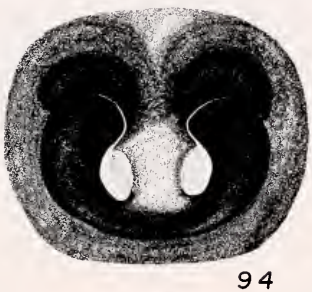

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Figs. 99–100. *Hamataliwa circularis* (Kraus), female holotype from 6 km N of Las Blancos, El Salvador, genitalia mounted in glycerine gel. 99. Ventral view. 100. Dorsal view.

Figs. 101–102. *Hamataliwa bufo* sp. n., female from Barro Colorado Island, Panama Canal Zone, 3–5 July 1936. 101. Internal genitalia. 102. Epigynum.

Fig. 103. *Hamataliwa bufo* sp. n., epigynum of female holotype from Barro Colorado Island, Panama Canal Zone, 1–4 July 1950.

Fig. 104. *Hamataliwa tricuspidata* (F.O.P.-Cambridge), internal genitalia of female from Arraijan, Panama, 6–9 July 1950.

Fig. 105. *Oxyopes clypeatus* F.O.P.-Cambridge = *Hamataliwa tricuspidatus*, epigynum of female holotype from Bugaba, Panama.

Fig. 106. *Hamataliwa tricuspidatus* (F.O.P.-Cambridge), epigynum of female from Arraijan, Panama, 6–9 July 1950.

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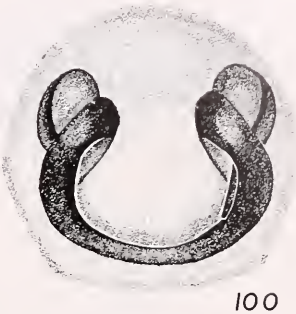

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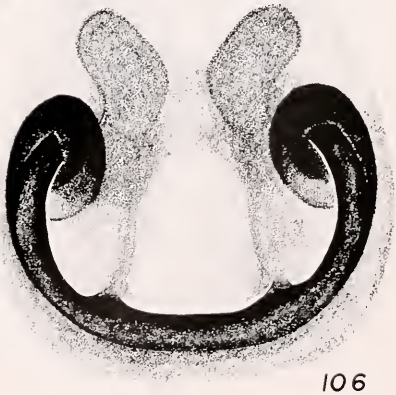

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Figs. 107–108. *Hamataliwa hista* sp. n., male holotype from Boquete, Panama, 4–11 Aug. 1954. 107. Left palpus, ventral view. 108. Left palpus, retralateral view.

Figs. 109–110. *Hamataliwa cavata* (Kraus), male holotype from San Salvador, El Salvador, Nov. 1951. 109. Palpus, ventral view. 110. Palpus, retralateral view.

Figs. 111–112. *Hamataliwa ursa* sp. n., male holotype from Barro Colorado Island, Panama Canal Zone, June 1950. 111. Palpus, ventral view. 112. Palpus, retralateral view.

Figs. 113–115. *Hamataliwa puta* (O.P.-Cambridge), male lectotype from Bugaba, Panama. 113. Palpus, ventral view. 114. Tibia of palpus. 115. Palpus, retralateral view.

Figs. 116–119. *Hamataliwa puta* (O.P.-Cambridge), poralectotypes from Bugaba, Panama. 116. Palpus, ventral view. 117. Tibia of palpus. 118. Palpus, retralateral view. 119. Tibia of palpus, second paralectotype. Figures 114, 117, 119 demonstrate variability in tibial apophyses of palpi.

Scale is for *all* palpi.

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Figs. 120–121. *Hamataliwa triangularis* (Kraus), male from Barro Colorado Island, 23–30 June 1939. 120. Left palpus, ventral view. 121. Left palpus, retrolateral view.

Figs. 122–123. *Hamataliwa globosa* (F.O.P.-Cambridge), male holotype from Bugaba, Panama. 122. Palpus, ventral view. 123. Palpus, retrolateral view.

Figs. 124–125. *Hamataliwa flebilis* (O.P.-Cambridge), male holotype from Bugaba, Panama. 124. Palpus, ventral view. 125. Palpus, retrolateral view.

Figs. 126–127. *Hamataliwa crocata* sp. n., male holotype from Summit, Panama Canal Zone, 23–28 Aug. 1950. 126. Palpus, ventral view. 127. Palpus, retrolateral view.

Figs. 128–129. *Hamataliwa tricuspidata* (F.O.P.-Cambridge), male holotype from Bugaba, Panama. 128. Palpus, ventral view. 129. Palpus, retrolateral view.

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Bulletin OF THE
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The Spider Family Oecobiidae in North America, Mexico, and the West Indies

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CAMBRIDGE, MASSACHUSETTS, U.S.A.

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THE SPIDER FAMILY OECOBIIDAE IN NORTH AMERICA, MEXICO, AND THE WEST INDIES

WILLIAM A. SHEAR*

ABSTRACT

Two genera of the spider family Oecobiidae are recognized as occurring in the area studied: *Oecobius* Lucas, 1846, and *Platoecobius* Chamberlin and Ivie, 1935. The genera *Omanus* Thorell, 1870, *Thalamia* Hentz, 1850, *Ambika* Lehtinen, 1967, and *Tarapaca* Lehtinen, 1967, are synonyms of *Oecobius*. The female of *O. beatus*, the male of *P. floridanus*, and mature specimens of *O. isolatus* are described for the first time. *Oecobius interpellator*, *O. bracae*, *O. juangarcia*, *O. civitas*, *O. piaxtla*, *O. rivula*, *O. culiacanensis*, and *O. isolatoides* are described as new. The social behavior of *O. civitas* is briefly described.

INTRODUCTION

Members of the family Oecobiidae are listed in nearly every faunal survey of North American spiders, primarily on the basis of one or two widespread, synanthropic species. An examination of the tropical and subtropical Mexican fauna for this study has increased the number of known species in the region from six to fifteen, most of which are well established apart from human dwellings.

Except for the ubiquitous *Oecobius annulipes* Lucas, little is known of the habitats of these minute cribellate spiders. Debski (1922) published a few ecological observations on *Oecobius templi* O. P.-Cambridge, in Egypt. He found webs stretched over small projections on walls and on the bark of *Eucalyptus* trees; the major item of prey seemed to be ants. Millot (1931, 1938) studied the anatomy of the spinning apparatus of *Oecobius cellariorum* (Dugès) in great detail, but did not publish any observations on how these organs were used by the spider.

Most valuable is a recent study by Glatz (1967) on the web construction, feeding behavior, and mating of *O. annulipes*. Glatz found that in southern France, *O. annulipes* constructs two kinds of webs, one of an irregular starlike shape, and another, more tubular type. I have observed the first type constructed by specimens of *O. annulipes* in Torreya State Park, Liberty County, Florida. The main food of the French specimens was found to be two species of ants, *Plagiolepis pygmaea* and *Lasius flavus* (Glatz, 1967); in Florida I observed the spiders feeding on minute Diptera. Of great interest are Glatz's observations on the use of *Oecobius*' extraordinary anal tubercle. The stout, curved bristles with which the apical joint of the anal tubercle is ringed are used to comb the silk from the large posterior spinnerets, much as other cribellate spiders card silk from the cribellum with the calamistrum on the metatarsus of the fourth legs. Only rarely did Glatz observe *O. annulipes* using cribellar silk to swath prey.

Copulation takes place in a special mating web constructed by the male. The

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male takes a position facing the female and slightly beneath her, and inserts the right palpus into the left side of the female epigynum, and vice versa, five or more times. Each egg sac contains three to ten eggs, which receive no protection or care from the female after they are laid (Glatz, 1967).

Several partly synanthropic species, such as *O. putus, O. concinnus,* and *O. beatus,* presumably exhibit similar behavior under stones and in leaf litter or on plants.

Of considerably greater interest is the large number of new species ranging from northern Arizona to Oaxaca. While many of these species are to be found in situations similar to that described for *O. annulipes* (when living apart from man), at least one, *O. civitas,* is known to be communal. The great numbers of individuals comprising single collections of *O. culiacanensis* and *O. rivula* point to a possible communal existence for these species also.

The synanthropic or partly synanthropic species of *Oecobius* are widely distributed. *Oecobius annulipes* is known from North and South America, Europe, North Africa, Southeast Asia, and numerous oceanic islands. *Oecobius concinnus* occurs in the West Indies to the exclusion of other oecobiids, and has also been found in peninsular Florida, Venezeuela (Simon, 1892) and coastal Mexico. Records of this species in the literature (as *O. nieborowskii*) include Costa Rica (Kulczyinski, 1909, type of *O. nieborowskii,* illustrated) and the Galapagos Islands (Banks, 1931). In contrast, the "native" American species are often quite local, although more intensive collecting may show them to be widely distributed. *Oecobius isolatus* is found only in Baja California and the lower Colorado River basin; *O. culiacanensis* is limited to central Sinaloa and western Durango.

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TAXONOMY

OECOBIIDAE

Oecobiidae Blackwall, 1862, Ann. Mag. Nat. Hist., 3(9) 382. Family Oecobiidae including only the type genus *Oecobius* Lucas, 1846.

Omanoidae Thorell, 1869, Nova Acta Reg. Soc. Sci. Upsaliensis, 3: 44. Type genus *Omanus* (= *Oecobius,* objective synonym).

Oecobiinae Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 267. Subfamily under Uroteidae; Lehtinen, 1967, Ann. Zool. Fenn., 4: 303. Subfamily under Oecobiidae.

Note. Regardless of whether one considers *Uroctea* confamilial with *Oecobius* or not, the family name of the family including *Oecobius* must be Oecobiidae, a family name which antedates Urocteidae Thorell, 1869, by seven years. Until more detailed investigations are carried out on the structure and development of the cribellate *Oecobius* and the ecribellate

Uroctea, I feel it is best to maintain the two separate families.

Diagnosis. Oecobiidae are separated from all other families of spiders except Urocteidae by the large, two-jointed anal tubercle with a double fringe of curved hairs. They may be separated from the Urocteidae by the possession of a cribellum and calamistrum.

Description. Cribellate spiders of the suborder Labidognatha. Respiratory system–pair of book lungs at base of abdomen and single tracheal spiracle opening immediately in front of cribellum. Spinnerets six, set close together, median pair smallest, posterior pair largest, with apical joint long, pointed, turned dorsally. Cribellum partially divided distally. Anal tubercle large, movable, two-jointed, with fringe of long, simple, sinuate hairs around base of apical joint; apical joint tipped with long sensory hairs. Carapace suboval to reniform, usually wider than long. Chelicerae small, without boss, convergent and touching throughout their length; fang minute, fang groove and cheliceral teeth lacking. Labium wider than long, free. Endites convergent over labium, almost touching. Sternum heart-shaped, wider than long, pointed posteriorly, separating posterior coxae. Eight eyes, in two rows, AME dark, PLE dark or light, others degenerate. Three claws, paired claws with single row of teeth, median claw small, accessory claws present; female pedipalp with single toothed claw. Calamistrum somewhat suppressed, in double series, absent in males. Female copulatory organ of the entelegyne type, one or two pairs of spermathecae present, opening directly into vaginal area or by means of copulatory tubes. Male palpus complex, pre-embolic sclerites suppressed, males with fringe of specialized spatulate hairs on sternal margin.

As regards non-genitalic characters, the members of the family are remarkably uniform, though several general trends of variability may be noted. Carapace shape varies from nearly round to reniform, and seems to be correlated with body size–larger species having comparatively broader and flatter carapaces. There are considerable age and sexual differences in carapace shape as well. Juveniles and males have much rounder, higher carapaces than adult females of a given species, and the carapace of the males of some species is modified for muscle attachments of the massive palpi. This modification usually takes the form of two lunate depressions on either side of the carapace. Macrosetae associated with the eyes have an arrangement characteristic of each genus studied, and will be described below. The legs lack macrosetae in most of the species, but some rather strong setae appear on the legs of larger species, and this character also appears to be correlated with size. Additional secondary sexual characters in the males are the lack of a calamistrum and great reduction of the cribellum, and the presence on the margins of the sternum of strong, spatulate hairs of unknown function.

The most important non-genitalic character of the oecobiids is the remarkable anal tubercle. This large, two-jointed, movable structure has been described in detail by Millot (1931, 1938), and by Glatz (1967). The possibility of the anal tubercle and the elongated posterior spinnerets replacing the calamistrum and cribellum respectively has already been mentioned. The loss of the calamistrum in males and the poorly differentiated nature of this structure in females provides additional evidence for this view.

To my knowledge, the only species erroneously placed in the Oecobiidae is "*Oecobius*" *sapporensis* (Saito, 1934). Although specimens were not available for study, it is clear from the excellent color figures that the type specimen is probably a theridiid. Yaginuma (1962) was the first to point out the erroneous placement of this species, but his paper was overlooked by Kritscher (1966), who included *sapporensis* in *Oecobius*.

KEY TO OECOBIID GENERA OF THE WORLD

1a. Tibia I about six to seven times longer than wide; calamistrum running two-thirds the length of metatarsus IV ..... *Oecobius*. p. 135

1b. Tibia I about four times longer than wide; calamistrum running entire length of metatarsus IV ..... *Platoecobius*. p. 161

THE GENERIC PROBLEM IN OECOBIIDAE

As is usual in spiders, different oecobiid genera and species are separated primarily by distinctions in the genitalia and eye patterns.

The eyes in species of *Oecobius* assume two distinct patterns. In the majority of species in the genus, the eyes are arranged in two straight to slightly procurved rows, with the posterior lateral eyes the largest, followed, in order of size, by the anterior medians, anterior laterals, and posterior medians. The anterior laterals and posterior medians are opalescent and irregular in shape (Fig. 14). In *O. putus* and *Platoecobius floridanus*, the rows are more distinctly procurved and the anterior medians are largest, followed, in order of size, by the posterior laterals, the anterior laterals, and the posterior medians. The anterior laterals and posterior medians are irregular and opalescent, and the posterior laterals are round, but light in color (Figs. 17, 27). *Oecobius cellariorum* (Fig. 13) has a pattern that is variable, but usually intermediate between these two.

The palpal organs of male *Oecobius* appear simple and easily described in the contracted state, but treatment of the palpus with an expanding agent reveals considerable complexity. The most obvious unusual feature of *Oecobius* male palpi is the extensive elaboration of the embolic division. The apparent tegulum in an unexpanded palpus is in reality the much enlarged radix, or basal part of the embolus. In the more complex representatives of the genus, the embolus is further subdivided, forming three distinct sclerites. Homologies in such an unusual palpal type cannot clearly be established, but it is useful to apply the same terms to structures that are analogous in other spider groups. The terms used here are based on those originated by Comstock (1940), and further described by Shear (1967). The order in which the following descriptions are arranged is not intended to suggest a possible phylogeny, rather, simpler palpi are described first.

Oecobius putus shows most of the features common to the palpi of a majority of the species of *Oecobius*. In a lateral view of an extended palpus (Fig. 1), the tegulum (*t*) can be seen to articulate with the enlarged basal part of the embolus, which may be termed the radix (*r*), by means of a strong sclerotized rod fitting into an internal socket (possibly this rod could be called a median apophysis). The conductor (*c*) is large and complex. In a mesal view (Fig. 2), the incomplete, spiral nature of the radix is revealed, and the articulation between the basal part and the intromittent portion of the embolus (*e*) is clear.

Oecobius cellariorum, the type species of the genus, differs from *O. putus* only in that the intromittent portion of the embolus (*e*) bears a large curved hook near its articulation with the radix (*r*). The actual intromittent portion of the embolus cannot be seen in either of the figures (Figs. 3, 4), but is a short, slightly curved spine.

The palpus of *O. concinnus* (Figs. 5, 6) is more complex than the preceding two examples. The large, curved hook of the embolus is present as a separate sclerite, which can be designated the stipes (*s*). The distal portion of the embolus (*e*) articulates with the stipes and not with the radix (*r*). The radix bears a thin sclerotized rod on its lateral surface. The conductor (*c*) is reduced in size.

Oecobius rivula (Figs. 7, 8) is representative of a group of Mexican species whose palpi differ in a few particulars from *O. concinnus*. The process of the radix (*r*) is present in this group as a thick,

heavy apophysis (radical apophysis, *a*), and the radix is reduced in size. The stipes (*s*) is enlarged mesally. The distal portion of the embolus is a small, curved spine (*e*). Of some interest is the perforation in the stipes of these species, opposite the median apophysis of the tegulum (*t*).

In *O. annulipes* (Figs. 9, 10), a similarity to the *O. putus-O. cellariorum* plan is obvious. The embolus (*e*) and conductor (*c*) are subequal in size, and the radix (*r*) is a spiral making slightly more than one turn.

In *Platoecobius floridanus*, illustrated in Figures 11 and 12, the palpus is simpler than in *O. annulipes*. The tegulum (?) may be represented only by a ringlike patch of slightly heavier sclerotization on the basal hematodocha (*bh*). The spiral radix (*r*) is much enlarged and makes one and one-half full turns. The conductor (*c*) is small and partly membranous. The stipes (*s*) is also small, but bears a distal hook opposite its articulation with the intromittent part of the embolus (*e*). The track of the sperm tube inside the palpus is much convoluted, and is valuable in ascertaining the relationships of the sclerites.

The female genitalia may be discussed from two aspects, external and internal. Externally, features common to most species of *Oecobius* are a scape of extremely variable size and shape, and a large, common fossa from which the openings of the copulatory ducts lead to the spermathecae. In *O. annulipes* (Fig. 29), the scape is long and narrow, while in *O. civitas* (Fig. 43), *O. isolatus* (Fig. 35), *O. isolatoides* (Fig. 37), and related Mexican species, the scape is broad. In each of these, however, the fertilization tubes are plainly visible, and they open at the distal end of the scape, or into notches that run to the distal end of the scape (*O. culiacanensis*, Fig. 45). In *O. cellariorum* (Fig. 28), *O. beatus* (Fig. 33), and *O. bracae* (Fig. 41), the scape is very broad and short, but otherwise comparable to the above species. A slightly different pattern occurs in *O. concinnus* (Fig. 31), *O. juangarcia* (Fig. 40), and *O. rivula* (Fig. 39). The scape is folded anteriorly, then somewhat posteriorly, and the fertilization tubes open into or near a common fossa that may be set back from the distal margin of the scape. *Oecobius interpellator* (Fig. 36) is apparently not very closely related to the other species studied here; both a scape and common copulatory fossa are absent. *Platoecobius floridanus* (Fig. 46) departs radically from this basic external pattern by being practically devoid of any external epigynal modifications, except for an anterior sclerotized notch of unknown function.

Internally, the basic pattern in *Oecobius* shows little variation. The copulatory ducts vary in length; in *O. annulipes* (Fig. 30) and *O. civitas* (Fig. 44) they are moderately long, but in *O. bracae* (Fig. 42) and *O. concinnus* (Fig. 32) they are practically nonexistent. The spermathecae are heavy-walled, and vary in shape from rather rounded (*O. civitas*, Fig. 44) to more elongate (*O. concinnus*, Fig. 32). In species with long copulatory ducts, the spermathecae are always lateral to the copulatory openings, except in *O. annulipes* (Fig. 30), where they are anterior and mesal. The fertilization tubes are long in all species, and traverse the scape for at least the distal third of their length.

Once again, *Platoecobius floridanus* (Fig. 47) differs considerably from the other oecobiids studied. The heavy-walled primary spermathecae are sessile and posterior to the copulatory openings. Connecting ducts run laterad and anterior to open into large, weakly sclerotized secondary spermathecae, from which they continue mesoposteriad as fertilization tubes to open, without external modification, on the ventral surface of the abdomen anterior to the copulatory openings.

Recently, Lehtinen (1967) has divided the family Oecobiidae into six genera, of which three are new. Two of the three

genera are monotypic. *Thalamia* is resurrected from synonymy, and *Platoecobius* Chamberlin and Ivie 1935, is retained. An examination of the chart (Lehtinen, 1967: 304) in which the characters of the proposed genera are given reveals that the new genera are erected primarily on the grounds of differences in the eyes and genitalia.

Examples of characters in the chart are such items as abdominal color pattern, which I believe can vary with feeding and the reproductive state of the spider, the presence of strong leg macrosetae and trichobothrial distribution, [which Lehtinen (1967: 305) indicates "... are easily explained by the general correlation of these characters to the average size of the spiders."], and a series of other characters that are uniform throughout the family. In addition, errors of observation and interpretation have crept in; the "fovea" (thoracic groove) of all oecobiids examined by me was very shallow and transverse, yet Lehtinen (1967) lists five different forms, ranging from "totally absent" to "long and rather deep." The comments on genitalia are filled with terms not explained nor illustrated. The genus *Oecobius sensu* Lehtinen is said to be Mediterranean in distribution, but includes *O. formosensis* Kishida, of the Orient, and *O. cellariorum*, synanthropically widespread in Europe and North America; *Platoecobius* is said to be distributed through the "N. Neotropical– S. Nearctic" regions, but the only species, *P. floridanus* (Banks), is known only from Florida, Georgia, and South Carolina in the United States. In addition, three of the genera are based on a knowledge of only the female sex of the included species.

The discussion of eye characters and genitalia above delimits the ranges of variability in the fifteen species and nearly 1500 specimens studied by me, including both sexes in all cases. Certainly, the eye arrangement of *Oecobius putus*, for example, selected by Lehtinen as the type species of *Ambika*, is distinct from that of most other members of *Oecobius sensu latu;* but in many of the males of *Oecobius cellariorum*, type species of *Oecobius*, a similar pattern with enlarged anterior median eyes, is found. Clearly, *O. putus* is not in any other way except eye arrangement related to *Platoecobius floridanus*, but its genitalia are quite within the range of variation of *Oecobius*. Thus it would seem that eye pattern is subject to convergence in otherwise unrelated species. Perhaps similar habits, as yet undescribed, provide the selection pressures producing this convergence. The genitalia of *O. nieborowskii* (= *O. concinnus* Simon), type species of Lehtinen's genus *Tarapaca*, also fall within the variation found in *Oecobius*.

Most modern taxonomists feel that the genus represents a group of closely related species that occupy a similar ecological niche and may be separated from other such groups by a distinct morphological discontinuity, although this latter criterion is often soft-pedalled (Mayr, Linsley, and Usinger, 1953: 57–59; Mayr, 1963: 588–592). It has also been emphasized that the criteria by which genera are delimited are essentially subjective, and that little is gained by splitting long-recognized, seemingly natural higher taxa (Mayr, Linsley, and Usinger, 1953: 59). Taking this into account, along with the evidence of the similar genital pattern of *Oecobius* species presented above, it is my opinion that three of Lehtinen's genera, *Ambika*, *Tarapaca*, and *Thalamia*, must be considered synonyms of *Oecobius*. I have refrained from commenting on the genus *Maitreja* Lehtinen 1967, type species *Maitreja marathaus* (Tikader), from India, since I have been unable to examine any specimens of this species, but the published figures (Tikader, 1962) do not seem to warrant the retention of *Maitreja* as a generic name. Indeed, *M. marathaus* may be a synonym of *O. cellariorum*.

However, after studying in detail the general structure and genitalia of *Platoecobius floridanus* including, for the first time, male specimens, I concur with Chamberlin and Ivie (1935) and Lehtinen (1967) that it deserves generic recognition. In addition to its unique genitalia, it is the only oecobiid known not to weave a web for capture of prey (Chamberlin and Ivie, 1935), thus occupying a distinct ecological niche. Therefore, two genera, *Oecobius* Lucas 1846 and *Platoecobius* Chamberlin and Ivie 1935, are recognized from the area of this study.

Genus *Oecobius* Lucas 1846

Oecobius Lucas, 1846, Expl. Sci. Algérie, Zool. I, Arach., p. 100, type species designated by Thorell, 1869, (On European Spiders, p. 112), *Oecobius domesticus* Lucas (= *O. cellariorum* (Dugés); Simon, 1875, Arach. France, 2: 6; 1892, Ann. Entomol. Soc. France, p. 435; Comstock, "1912" (1913), The Spider Book, p. 288; Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 267; Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 499; Kaston, 1953, How to Know the Spiders, p. 36; Lehtinen, 1967, Ann. Zool. Fenn., 4: 253, p. 304.

Omanus Thorell, 1870, Nova Acta Reg. Soc. Sci. Upsaliensis, ser. 3, p. 114, type species by original designation *Oecobius navus* Blackwall (= *O. annulipes* Lucas); Keyserling, 1891, Die Spinnen Amerikas, Vol. 3 (Brasilianische Spinnen), p. 160.

Thalamia Hentz, 1850, J. Boston Soc. Nat. Hist., 6: 35, type species by monotypy *Thalamia parietalis* Hentz (= *O. annulipes* Lucas); Banks, 1890, Proc. Entomol. Soc. Washington, 2: 125; Lehtinen, 1967, Ann. Zool. Fenn., 4: 269, 304.

Ambika Lehtinen, 1967, Ann. Zool. Fenn., 4: 212, 304, type species by monotypy *Oecobius putus* O. P.-Cambridge. NEW SYNONYMY.

Tarapaca Lehtinen, 1967, Ann. Zool. Fenn., 4: 267, 304, type species by monotypy *Oecobius nicborowskii* Kulczynski (= *O. concinnus* Simon). NEW SYNONYMY.

Diagnosis. *Oecobius* is separated from *Platoecobius*, the only other genus in the family, by having longer, thinner legs, the calamistrum of the females extending two-thirds the length of metatarsus IV, and the more complex genitalia.

Description. Small oecobiid spiders (1.5–4.5 mm total length) with characters of the family. Carapace with sides rounded, clypeus prolonged into subtriangular projection. Carapace flat to moderately high, head region moderately elevated. Eyes on low tubercle, eye area wider than long. Anterior median eyes (AME) and posterior lateral eyes (PLE) round, dark; anterior lateral eyes (ALE) and posterior median eyes (PME) irregular, light. Macrosetae of eye area as follows: three between AME, one behind each PME, two nearly contiguous on midline behind eye area; position of macrosetae varying somewhat with eye arrangement of species. Thoracic groove transverse, absent to indistinct. Carapace depressed and indented above pedicel. Abdomen flattened, elongate to suboval, somewhat pointed behind. Leg formula usually 4213 or 421=3. Legs long, thin, spines weak to lacking, without definite arrangement. Tarsi without trichobothria, metatarsal trichobothria one or two, without definite arrangement. Hind coxae separated by sternum. Calamistrum lacking in mature males, extending in immature specimens and females along proximal two-thirds of metatarsus IV. Palpi of mature males with tegulum and subtegulum greatly suppressed, visible only in treated palpi, conductor large, well sclerotized, embolus consisting of two or three sclerites, intromittent portion a short, curved spine. Female with more or less elaborate epigynal modification, one pair of heavily sclerotized spermathecae.

Fourteen species are known from the region of this study; most of them are very similar, and best separated by reference to the figures. Only the most significant references are given under each species; for more detailed references, see Roewer (1954), and Bonnet (1958).

Key to Species of *Oecobius*:

1a. AME larger than or equal to PLE (Figs. 13, 17) ..... 2.

1b. AME five-sixths the diameter of PLE, or smaller (Fig. 16) ..... 3.

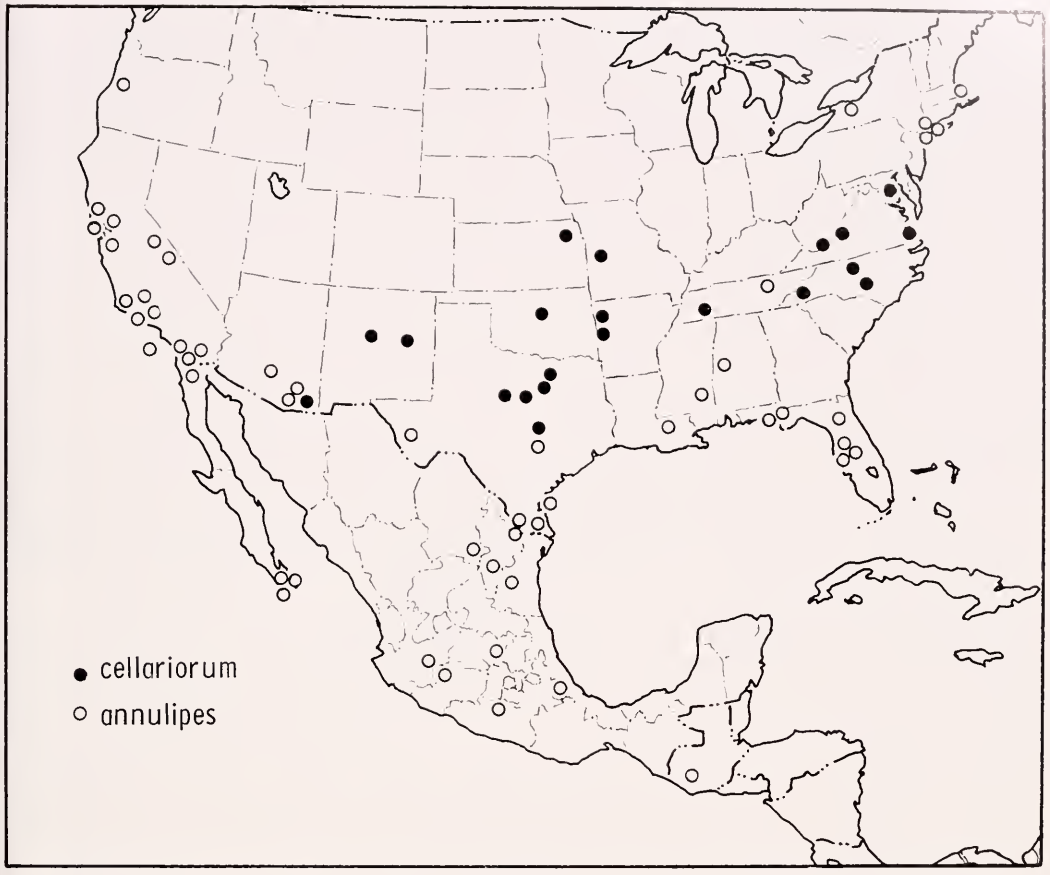
2a. Eye area nearly twice as wide as long, or wider (Fig. 17); PLE pale but not opalescent ..... *putus.* p. 144
2b. Eye area nearly square (Fig. 13); PLE dark ..... *cellariorum.* p. 136
3a. Carapace yellowish white, unmarked, or with dark markings on a yellowish white ground (Figs. 13, 16) ..... 4.
3b. Carapace medium brown to black, lighter individuals with a dark pattern (Figs. 18, 22) ..... 9.
4a. Carapace unmarked except for marginal dark line and often a dusky central band (Fig. 13) ..... *cellariorum.* p. 136
4b. Carapace with additional markings, usually taking the form of three dark spots on each side (Figs. 14, 15), or of submarginal bands (Figs. 20, 24) ..... 5.
5a. Submarginal spots well separated from each other and from marginal line (Figs. 14, 15) ..... 6.
5b. Submarginal spots fused to each other (Fig. 24), or to marginal line (Fig. 20), or both ..... 8.
6a. Epigynum without a scape (Fig. 36); male palpus in lateral view with a large, serrate, distally hooked conductor (Fig. 58); Cambridge, Mass., and New Caledonia (?) ..... *interpellator.* p. 146
6b. Not as in 6a ..... 7.
7a. Submarginal spots *usually* commalike, nearly touching (Fig. 15); epigynal scape broader than long (Fig. 31); male palpus with a large stipal process in mesal view (Fig. 52); West Indies, Florida, coastal Mexico, Central America, Venezuela, Columbia ..... *concinnus.* p. 141
7b. Submarginal spots oval, well separated (Fig. 14); epigynal scape three to four times longer than broad (Fig. 29); stipal process of male palpus small (Fig. 51); pantropical, north to Massachusetts and Oregon on the North American coasts ..... *annulipes.* p. 138
8a. Submarginal spots usually connected to form a submarginal band which is then connected to the marginal line (Fig. 24); epigynal scape squared-off posteriorly and notched (Fig. 41); male palpus as in Figure 70; Oaxaca ..... *bracae.* p. 156
8b. Submarginal spots usually separated from each other, but connected to marginal line (Fig. 20); epigynum with a very short, broad scape bearing two posterior digital processes (Fig. 33); male palpus as in Figure 54; Guerrero, Tamaulipas ..... *beatus.* p. 143
9a. Carapace of adults evenly dark brown to black (Fig. 23), immatures more lightly colored, often marked darker; epigynal scape with a central depression (Fig. 40); male palpus lacking radical apophysis (Fig. 67; compare with Fig. 69); Oaxaca ..... *juangarcia.* p. 154
9b. Carapace of adults dark to light brown, but generally with a much darker pattern or shading (Figs. 18, 19, 21); epigynal scape without a central depression; male palpus with radical apophysis (except for *O. civitas,* Figs. 72, 73) ..... 10.
10a. Epigynal scape as wide or wider than long, *not distinctly narrowed distally* (Fig. 43); male palpus without a radical apophysis (Figs. 72, 73); west-central Mexico ..... *civitas.* p. 157
10b. Epigynal scape longer than wide, or *if not, then distinctly narrowed distally;* male palpus with radical apophysis ..... 11.
11a. Epigynal scape as wide or wider than long, distinctly narrowed distally (Fig. 38); male palpus as in Figures 64, 65; Sinaloa ..... *piaxtla.* p. 150
11b. Epigynal scape longer than wide, narrowed distally or not (Figs. 35, 37); male palpus not as in Figures 64, 65; ..... 12.
12a. Fertilization tubes opening into distal notches on epigynal scape (Fig. 45), scape not narrowed distally; male palpus as in Figures 74, 75; Sinaloa ..... *culiacanensis.* p. 159
12b. Fertilization tubes not opening into distal notches; male palpus not as in Figures 74, 75 ..... 13.
13a. Scape with a small perforation near tip, narrowed distally (Fig. 39); male palpus massive, as in Figures 68, 69; Sinaloa ..... *rivula.* p. 152
13b. Scape without such a perforation; male palpus otherwise ..... 14.
14a. Scape narrowed distally (Fig. 37); male palpus as in Figures 62, 63; Arizona, Sonora, N. Sinaloa ..... *isolatoides.* p. 150
14b. Scape not narrowed distally (Fig. 35); male palpus as in Figures 60, 61; lower Colorado River valley, Baja California ..... *isolatus.* p. 148

Oecobius cellariorum (Dugès)

Figures 3, 4, 13, 28, 48, 49; Map 1

Clotho cellariorum Dugès, 1836, Ann. Sci. Nat., 2: 161. Types presumed lost. Type locality not designated.

Oecobius cellariorum, Simon, 1875, Arach. France, 2: 7. Roewer, 1954, Katalog der Araneae, 2: 1288. Bonnet, 1958, Bibliographia Araneorum, 2: 3132. Kritscher, 1966, Ann. Naturhist. Mus. Wien., 69: 287, pl. 1, fig. 4, 5, 6, ♂ ♀.



Map 1. North America, showing distribution of O. *cellariarum* and O. *annulipes*.

Oecobius domesticus Lucas, 1846, Expl. Sci. Algérie, Zool. 1, Arach., 100–101, pl. 2, figs. 1a–1g, ♀. Types presumably in the Paris museum, not examined; type locality, Algiers, Algeria.

Oecobius texanus Bryant, 1936, Psyche, 43: 87, figs. 8a–8e, ♂ ♀. Male holotype, female paratypes from Dallas, Texas, in Museum of Comparative Zoology, examined. Gertsch and Mulaik, 1940, Bull. Amer. Mus. Nat. Hist., 97: 335. Muma, 1944, Amer. Mus. Novitates, 1257: 1. Roewer, 1954, Katalog der Araneae, 2: 1290. Bonnet, 1958, Bibliographia Araneorum, 2: 3135. NEW SYNONYMY.

Diagnosis. This species is distinguished from all other Nearctic species except *O. putus* by the virtually unmarked carapace, and from *O. putus* by the eye relations (*cf.* Figs. 13, 17) and the smaller size of *O. cellariorum.*

Description. Female from Las Cruces, New Mexico: carapace (Fig. 13) suboval, wider than long (L/W = 1/1.3), almost glabrous, pale hairs on margins and lateral to eye area. Clypeus slightly prolonged, steeply sloping, about ten degrees from vertical. Eye area highest point of carapace, sloping steeply to clypeus and laterally, prolonged behind almost to thoracic groove, then declining sharply to posterior margin of carapace. Eye area wider than long (L/W = 1/1.5), eyes in two rows, posterior row recurved, anterior row nearly straight. PLE the largest, dark, separated

by about two and one-half times their diameter; PME irregular, opalescent, separated by scarcely one-fourth diameter of PLE, and from each other by their diameter, nearly contiguous with PLE; ALE irregular, opalescent, nearly contiguous with AME. Labium subtriangular, wider at the base than long. Sternum longer than wide (L/W = 1/.83), anterior margin slightly excavated to receive labium, bluntly pointed behind, separating posterior coxae by slightly more than their width, clothed sparsely with long hairs, more dense around margins. Abdomen suboval, pointed behind, widest slightly anterior to middle of length, densely set with colorless hairs. Epigynum (Fig. 28) with two strongly chitinized lateral lobes overhanging a transversely wrinkled area.

Carapace pale yellowish white, except for dark marginal line, dusky area surrounding eyes; eyes ringed with black. Abdomen pale gray with chalky white blotches, except in cardiac area, three pairs of distinct dark spots marking abdominal apodemes. Venter pale gray blotched chalky white, spinnerets slightly darker. Endites, labium, sternum, and coxae of legs uniform pale yellowish white. Legs slightly darker distally, femoral bases off-white, tarsi somewhat dusky; vaguely indicated annuli median on femora and tibiae of anterior legs and distally on metatarsi. Total length, 2.90 mm. Carapace .90 mm long, 1.02 mm wide. Tibiae I–IV .83, .87, .84, .90 mm long, respectively. Metatarsi I–IV .78, .87, .84, .98 mm long, respectively.

Male from Las Cruces, New Mexico, with structure essentially as in female, except as follows: carapace proportionally wider than in the female; eye area higher; and clypeus more steeply sloping, nearly vertical. PLE reduced in size, subequal to AME. Legs longer and thinner than in female. Sternum margined with special hairs which are spatulate and darkened distally. Coloration as in female. Palpus as in Figures 48, 49. Total length, 2.18 mm. Carapace .67 mm long, .95 mm wide. Tibiae I–IV .82, .87, .92, .96 mm long, respectively. Metatarsi I–IV .82, .90, .92, 1.00 mm long, respectively.

Ecological Notes. In the southwest, this species is fairly common both in and out of buildings; in the more northerly parts of its range it is restricted to indoor habitats. Males in Texas and New Mexico mature in June, and disappear in August. Immature males with swollen palpi appear in October and December. Females mature outdoors in July, but persist indoors the year round. The mode of life is essentially that described by Glatz (1967) for *O. annulipes.*

Distribution. (Map 1) From extreme western New Mexico across Texas and Oklahoma to Arkansas, Missouri, and Kansas; in Tennessee, Maryland, and North Carolina in the east. Absent from most of the range of *O. annulipes.* Common in Europe, but probably more closely related to North American forms, and may have originated here.

Oecobius annulipes Lucas

Figures 9, 10, 14, 29, 30, 50, 51; Map 1

Oecobius annulipes Lucas, 1849, Expl. Sci. Algérie, Zool. I, Arach., 102, figs. 2a–2g, ♀; types probably in Paris museum, not examined; type locality, Algiers. Simon, 1875, Arach. France, 2: 9. Kritscher, 1966, Ann. Naturhist. Mus. Wien., 68: 285, pl. 1, figs. 1–3, ♂♀.

Thalamia parietalis Hentz, 1850, J. Boston Soc. Nat. Hist., 6: 35, pl. 15, fig. 16, ♀; types destroyed; type locality, "S. Alabama."

Oecobius parietalis, Simon, 1892, Histoire Naturelles des Araignées, 1: 247, figs. 192, 197, ♀. Emerton, 1909, Trans. Connecticut Acad. Arts Sci., 14: 212, pl. 7, figs. 1a–1e, ♂♀. Comstock,

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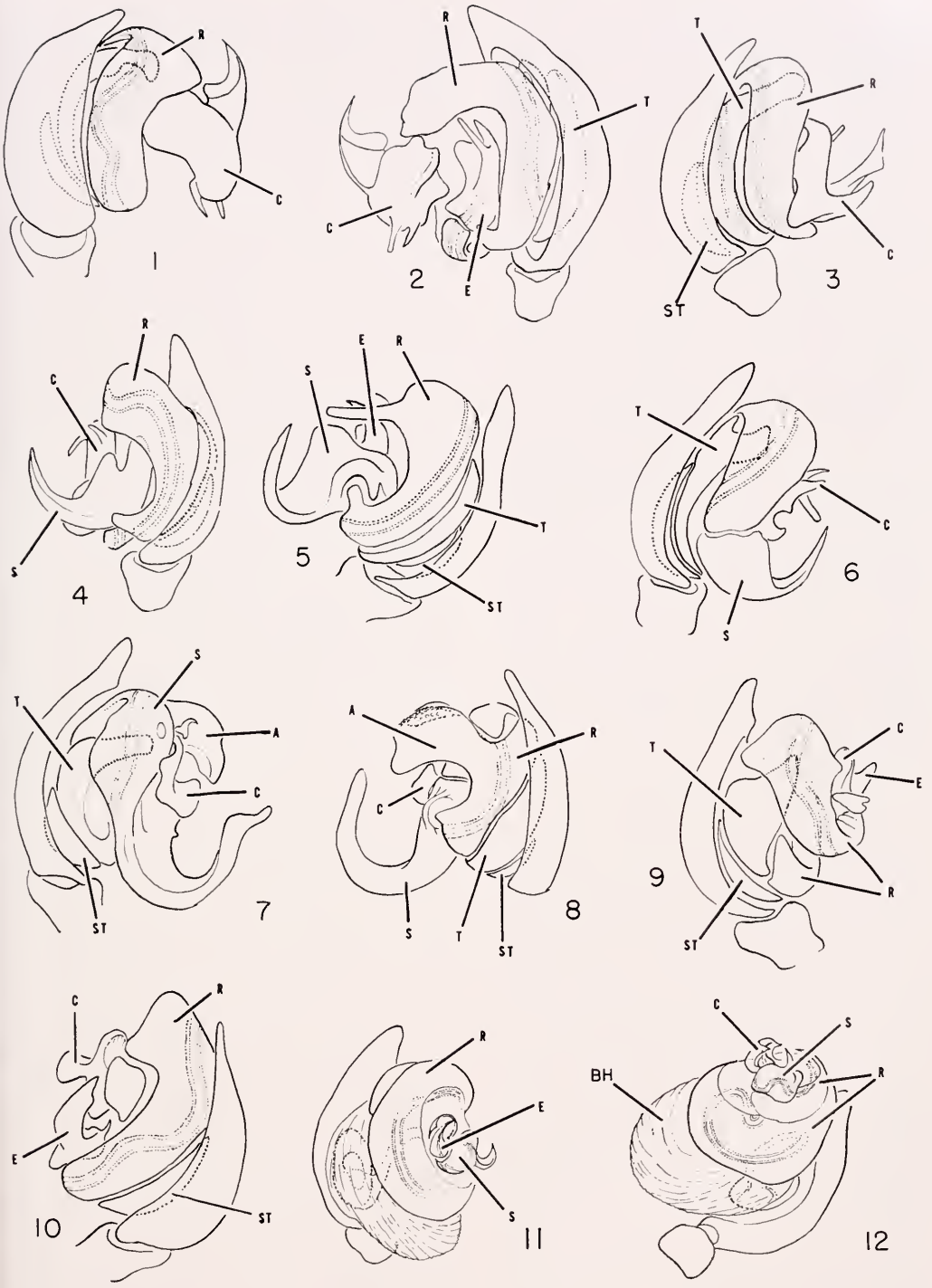
Expanded right palpi of males. Figs. 1–12. 1. *Oecobius putus,* lateral view. 2. *O. putus,* mesal view. 3. *O. cellariorum,* lateral view. 4. *O. cellariorum,* mesal view. 5. *O. concinnus,* lateral view. 6. *O. concinnus,* mesal view. 7. *O. rivula,* lateral view. 8. *O. rivula,* mesal view. 9. *O. annulipes,* lateral view. 10. *O. annulipes,* mesal view. 11. *Platoecobius floridanus,* lateral view. 12. *P. floridanus,* mesal view.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"1912" (1913), The Spider Book, p. 288, fig. 275, ♀. Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 267, figs. 1, 3–17, ♀ ♂. Kaston, 1948, Connecticut State Geol. Nat. Hist. Bull., 70: 599, pl. 101, figs. 1878–1881, ♀ ♂; Kaston, 1953, How to Know the Spiders, p. 36, figs. 69–70, ♀. Roewer, 1954, Katalog der Araneae, 2: 1288. Bonnet, 1958, Bibliographia Araneorum, 2: 3131–3132.

Diagnosis. The pattern of the carapace (Fig. 14) is characteristic, but similar to *O. interpellator* and *O. concinnus. Oecobius annulipes* is intermediate between these two in size. The palpus of *O. concinnus* (Fig. 52) has two large, projecting apophyses, and the epigynal scape (Fig. 31) is wider than long. An epigynal scape is lacking in *O. interpellator,* and the palpus is distinctive (Fig. 58). The palpus of *O. annulipes* (Fig. 50) is compact, without large projections, and the epigynal scape (Fig. 29) is long and pointed.

Description. Female from Sunland, California: carapace (Fig. 14) suboval, sparsely clothed with small hairs, wider than long (L/W = 1/1.3). Clypeus prolonged beyond eyes by one-tenth length of carapace and evenly rounded. Eye area wider than long (L/W = 1/1.3). PLE much the largest, separated by little less than two diameters. PME irregular, opalescent, nearly contiguous with PLE, separated by their greatest width. AME dark, about two-thirds diameter of PLE, separated from each other by a radius and from the PLE by a radius. ALE light, irregular, nearly contiguous with AME. Anterior eye row and posterior eye row of nearly the same width, both rows procurved so that anterior margin of PME is on line drawn through centers of PLE, and posterior edge of ALE is on line drawn through centers of AME. Epigynum as in Figures 29, 30, with prominent scape bearing two small openings at its distal end and traversed by pair of tubes, openings of epigynal ducts concealed at base of scape, running short distance internally to two seminal receptacles. Legs clothed with fine hairs, some plumose, weak spines arranged irregularly, strongest situated dorsally at distal ends of femora and patellae, and ventrally at distal ends of tibiae. Number of bristles found in calamistrum varies from specimen to specimen, lowest number found being 19, greatest 27, but in all cases inner row has greater number of bristles. Remainder of structure in close agreement with *O. cellariorum.* Carapace yellowish white, marginal band gray. Eyes surrounded by black rings blending off into gray area extending backwards and tapering to thoracic groove, then continuing as band as wide as groove to posterior margin of carapace. Anteriorly, gray area constricted between AME, widening abruptly, extending down clypeus, tip of clypeal projection light. Three dusky spots on carapace about midway between the marginal band and median dark area, opposite coxae of legs I, II, and III. Legs paler yellow, annulated as follows. Femur with two annuli, incomplete dorsally, one about middle of its length, other at distal end; patella dark ventrally; tibia with two annuli, incomplete dorsally; metatarsus with two annuli paler dorsally but complete; tarsi without annuli but slightly darker distally. Sternum, labium, endites, and coxae of legs uniform pale yellow; palpus dusky towards distal end. Abdomen grayish, mottled white, with darker, unmottled cardiac mark. Anterior margin of abdomen with dark band extending laterad about one-half length of abdomen, then replaced by three pairs of slanting dark marks that extend mesally almost to cardiac mark. Spinnerets and anal tubercle whitish, gray dorsally, surrounded by dusky area. Venter pale. Total length 2.91 mm. Carapace .70 mm long, .98 mm wide. Tibiae I–IV .83, .86, .82, .83 mm long, respectively. Metatarsi I–IV .74, .82, .83, .90 mm long, respectively.

Male from Sunland, California, with structure essentially as in female, except as follows. Carapace wider in proportion to its length (L/W = 1/1.4), clypeal projection slightly more acute. Eye area more

compressed, but only slightly wider in proportion to its length. Carapace more nearly glabrous than in female, but hairs of legs and sternum much longer. Abdomen much smaller in proportion to carapace, with longer hairs. Fringe on anal tubercle less well developed. Cribellum small. Calamistrum absent from fourth metatarsus. Color pattern less well developed than in female. Marginal band of carapace broken between coxae of legs, paired spots of carapace only faintly indicated, median dusky area limited to eye region and thoracic groove. Markings on abdomen fainter, dark coloration on dorsal side of apical segment of posterior spinnerets more pronounced. Palpus as in Figures 50, 51. Total length, 2.58 mm. Carapace .70 mm long, 1.05 mm wide. Tibiae I–IV .74, .81, .78, .81 mm long, respectively. Metatarsi I–IV .75, .78, .81, .85 mm long, respectively.

Ecological Notes. Discussed in detail by Glatz (1967) and in section INTRODUCTION above. Mature individuals are found throughout the year in houses. It has become established out-of-doors only in the southwestern United States and south into Mexico where it matures in early summer.

Distribution. (Map 1) Pantropical. I have examined specimens from Europe, India, South America, Africa, Hong Kong, South Viet Nam, and various oceanic islands, and found little variation. There is little evidence as to the point of origin of this highly synanthropic species.

Oecobius concinnus Simon

Figures 4, 5, 15, 31, 32, 52, 53; Map 2

Oecobius concinnus Simon, 1892, Ann. Entomol. Soc. France, p. 435, pl. 9, fig. 2, ♂; female holotype and male paratype from Puerto Cabello, Venezuela, in the Paris Museum, examined and photographed by J.-C. Ledoux. Roewer, 1954, Katalog der Araneae, 2: 1289. Bonnet, 1958, Bibliographia Araneorum, 2: 3133.

Oecobius nieborowskii Kulczynski, 1909, Bull. Internat. Acad. Sci. Cracovie, ann. 1909, sem. II, p. 454, pl. 22, fig. 30, ♀. Type locality Turrialba, C. R.; types not examined, disposition unknown. Roewer, 1954, Katalog der Araneae, 2: 1290. Bonnet, 1958, Bibliographia Araneorum, 2: 3134. NEW SYNONYMY.

Thalamia nieborowskii, Banks, 1931, Nyt Mag. Naturvidensk (Oslo), 118, p. 272, pl. 2, figs. 7, 8, ♂.

Oecobius benneri Petrunkevitch, 1929, Trans. Connecticut Acad. Arts Sci., 30: 75, figs. 64–66, ♀; female holotype from Rio Piedras, P. R., in American Musuem of Natural History, examined. Roewer, 1954, Katalog der Araneae, 2: 1289. Bonnet, 1958, Bibliographia Araneorum, 2: 3132. NEW SYNONYMY.

Oecobius vokesi Gertsch and Davis, 1942, Amer. Mus. Novitates, 1158: 19, Fig. 40, ♀; female holotype from 30 miles south of Jésus Carranza, Veracruz, in American Museum of Natural History, not examined, presumed lost. Roewer, 1954, Katalog der Araneae, 2: 1290. NEW SYNONYMY.

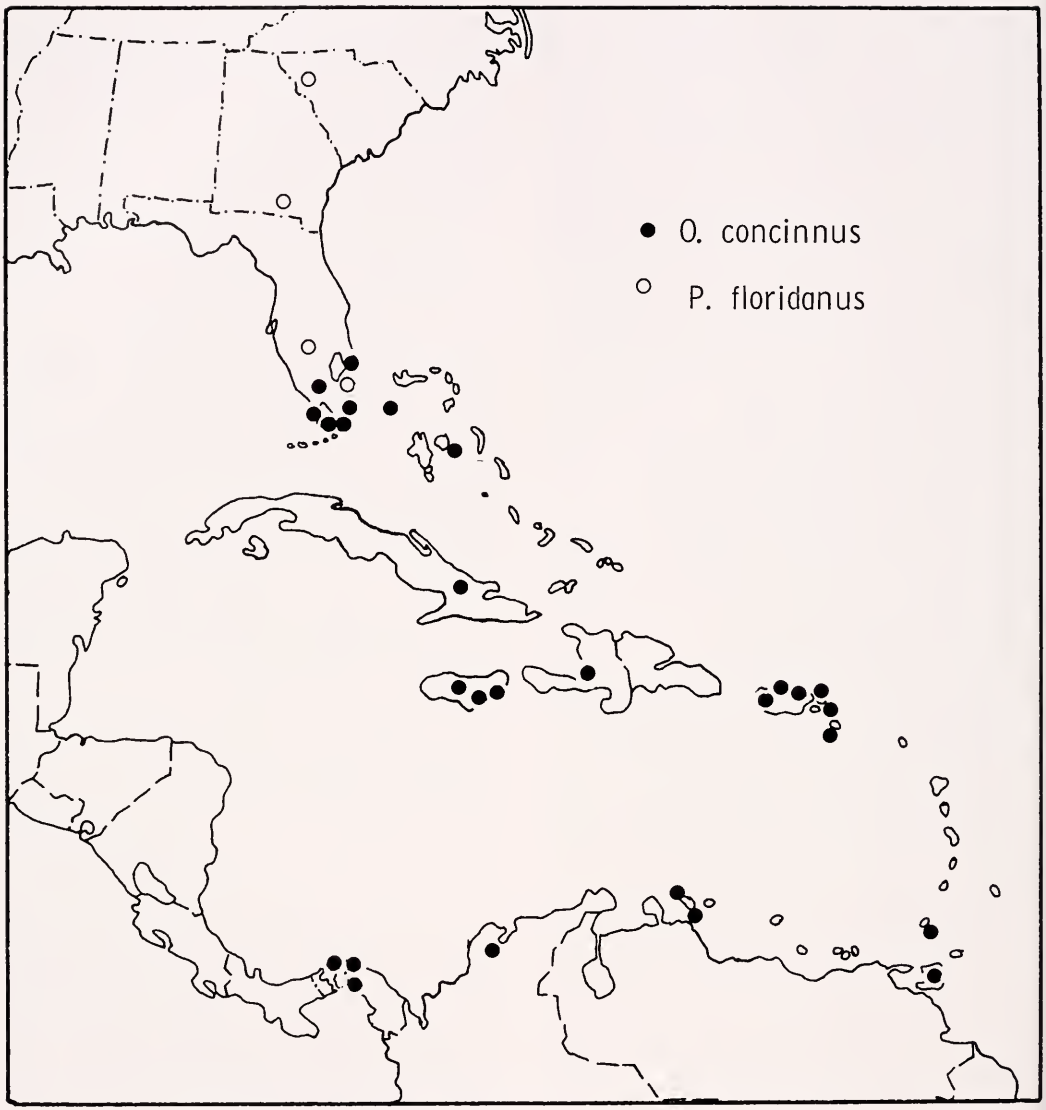
Oecobius audanti Bryant, 1948a, Bull. Mus. Comp. Zool., 100: 334, pl. 1, fig. 4, ♀, pl. 2, figs. 10, 12, ♂; male holotype, female paratype from Port-au-Prince, Haiti, in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Tarapaca nieborowskii, Lehtinen, 1967, Ann. Zool. Fenn., 4: 433, fig. 30, ♀.

Oecobius beatus, Bryant, 1948, Psyche, 55: 57, (in part) pl. 10, figs. 1, 2, ♂; specimen designated "allotype male" in Museum of Comparative Zoology, examined. Not *O. beatus* Gertsch and Davis, 1937, Amer. Mus. Novitates, 961, p. 2, figs. 1, 2, ♀; female holotype of *O. beatus* in American Museum of Natural History, examined. See *Oecobius beatus.*

Note. This species has accumulated the most impressive synonymy of any Nearctic-Neotropical species. The specimens designated as "allotypes" by Bryant (1948) belong to *O. concinnus,* while females found supposedly at the same place and time are typical *O. beatus.* A vial from the American Museum of Natural History from Tamaulipas contained *O. beatus* males and females. The synonymy of *O. vokesi* was established by the examination of specimens in the American Museum, verified by Dr. Gertsch. The placement of Banks' specimens is based on the close agreement between his figures and male specimens of *O. concinnus.*

Diagnosis. This species overlaps with others only in eastern Mexico and in Peninsular Florida, where it may be dis-



Map 2. Caribbean region, showing distribution of O. *concinnus* and P. *floridanus*.

tinguished from *O. annulipes* and *O. beatus* by reference to the figures, and the discussions under those species. No other species is known to occur in the West Indies, as Petrunkevitch (1929) observed in describing *O. benneri*.

Description. Female from St. Augustine, Trinidad: carapace (Fig. 15) suboval, wider than long (L/W = 1/1.2), clypeal projection evenly rounded; carapace highest in eye area and sloping evenly in all directions, more sharply posteriorly, glabrous, with a few plumose hairs. Eye area wider than long (L/W = 1/1.9), anterior eye row slightly procurved. PLE the largest, separated by one and one-third their diameter, PME irregular, opalescent, twice as long as wide, separated by one and one-

third their width, contiguous with inner margins of PLE. AME slightly more than one-half diameter of PLE, separated from each other by one and one-third diameters and from PLE by one-half diameter. ALE irregular, opalescent, contiguous with prolateral margins of AME. Epigynum as in Figures 31, 32. Remainder of structure typical. Carapace off-white, eyes ringed with black and surrounded by extensive dusky area. Clypeus entirely dusky, slightly lighter in center. Marginal line dark gray, three comma-shaped dusky marks contiguous end-to-end longitudinally between marginal line and central dusky area, faintly indicated gray spots extending towards these markings from marginal line. Abdomen grayish white, with a brown cardiac mark and brownish gray lines on sides. Venter mostly chalk-white, spinnerets light brown. Legs yellow-white with lateral maculae on coxae and trochanters of first two pairs, at midlength and distally on all leg segments except patellae and tarsi, patellae entirely dark laterally, tarsi somewhat darker distally. Maculae forming complete annuli on metatarsi. Total length, 1.37 mm. Carapace .68 mm long, .84 mm wide. Tibiae I–IV .60, .65, .60, .67 mm long, respectively. Metatarsi I–IV .48, .62, .62, .71 mm long, respectively.

Male from St. Augustine, Trinidad, with structure essentially as in female, except as follows: Abdomen smaller in comparison to carapace, carapace higher in eye area and sloping more sharply at posterior declivity. Eye area wider in proportion to length, AME slightly larger. Calamistrum lacking on metatarsus IV. Coloration somewhat paler than in female. Palpus as in Figures 52, 53. Total length, .92 mm. Carapace .65 mm wide, .77 mm long. Tibiae I–IV .53, .60, .55, .57 mm long, respectively. Metatarsi I–IV .45, .57, .54, .64 mm long, respectively.

Ecological Notes. This species is very common both inside and outside of buildings in the West Indies, and is the only species occurring there. The types of *O. audanti* and *O. benneri* were both taken in buildings. Bryant (1940) found this spider on garden foliage in Cuba; Dr. A. M. Chickering has collected literally hundreds of individuals from buildings. Mature males and females occur in the West Indies at all times of the year. The Florida specimens are all from areas of good tree cover, and only one was found on the outside of a building; the others were collected from under boards on the ground and under flakes of bark.

Map 3. Mexico and Southern United States, showing distribution of *O. beatus*, *O. putus*, and *O. civitas*.

Distribution. Islands of the Caribbean, Peninsular Florida, coastal Mexico, Central America, Venezuela, and Columbia (Map 2).

Oecobius beatus Gertsch and Davis

Figures 20, 33, 54, 55; Map 3

Oecobius beatus Gertsch and Davis, 1937, Amer. Mus. Novitates, 961: 2, figs. 1, 2, ♀; female holotype from Acapulco, Guerrero, in American Museum of Natural History, examined. Bryant, 1948, Psyche, 55: 57 (in part). Roewer, 1954, Katalog der Araneae, 2: 1289. Bonnet, 1958, Bibliographia Araneorum, 2: 1289.

Note. The "allotype male" so designated by Bryant (1948) in the Museum of Comparative Zoology is a male of *O. concinnus.*

The Acapulco females from a vial with the same data as the "allotype" are *O. beatus*. Specimens from Tamaulipas in the American Museum included true *O. beatus*, both males and females, and descriptions given here are based on those specimens.

Diagnosis. Distinguished by its small size and color from all other sympatric species except *O. bracae*, from which it may be separated by reference to the figures of the genitalia.

Description. Female from Rio Frio, Tamaulipas: carapace (Fig. 20) suboval, wider than long (L/W = 1/1.1), clypeal projection evenly rounded, with distinct shoulders at base of clypeus; carapace highest in eye area and sloping evenly in all directions, more sharply posteriorly, glabrous, with few scattered plumose hairs. Eye area wider than long (L/W = 1/1.6), eyes in two rows, both rows slightly procurved. PLE much the largest, separated by two and one-fourth times their diameter. PME irregular, opalescent, less than twice as long as wide, separated from each other by one and one-half times their greatest width, from ALE by their greatest width. AME round, dark, one-half diameter of PLE, separated from each other by two diameters, from PLE by one diameter. ALE irregular, opalescent, separated from AME by less than radius of AME. Epigynum as in Figure 33. Remainder of structure typical for the genus. Carapace yellow-white, PLE and AME ringed with black, dusky area surrounding eyes faint. Posterior part of carapace with irregular dusky band extending from just behind eye area to posterior margin, nearly discontinuous just anterior to thoracic groove, where it shows broad lateral extensions, "spectacle-like" light markings midway between thoracic groove and posterior margin of carapace. Clypeus light. Marginal band black, with dusky extensions at clypeal shoulder, three dusky extensions contacting three dark spots midway between central band and marginal line. Abdomen grayish white, with chalky blotches except in cardiac area. Dark brown markings nearly covering abdomen laterally and extending ventrally, leaving central light band on venter. Spinnerets and anal tubercle light, surrounded by dark area. Legs yellowish white, with annuli as in *O. concinnus*, but lighter and less distinct. Total length, 1.95 mm. Carapace .67 mm long, .74 mm wide. Tibiae I–IV .51, .50, .50, .52 mm long, respectively. Metatarsi I–IV .50, .51, .50, .56 mm long, respectively.

Male from Rio Frio, Tamaulipas, with structure and coloration essentially as in female, except as follows: carapace much wider in proportion to length (L/W = 1/1.14), larger in proportion to abdomen, flatter than in female, sloping more gradually from eye area. Eye area wider in proportion to length than in female (L/W = 1/2.6), eyes smaller, more dispersed. Legs proportionally somewhat longer than in female. Calamistrum absent from metatarsus IV. Palpus as in Figures 54, 55. Total length, 1.80 mm. Carapace .71 mm long, .81 mm wide. Tibiae I–IV .60, .56, .55, .60 mm long, respectively. Metatarsi I–IV .60, .56, .60, .64 mm long, respectively.

Ecological Notes. This species is found both on buildings and under stones.

Distribution. Tamaulipas, San Luis Potosí, Guerrero (Map 3).

Oecobius putus O. P.- Cambridge

Figures 1, 2, 17, 34, 56, 57; Map 3

Oecobius putus O. P.-Cambridge, 1876, Proc. Zool. Soc. London, p. 544–545, pl. 58, figs. 1a–1d, ♂; type specimens from ruined temple between Denderah and Assouan, additional material from Temple of Philae, Egypt. Roewer, 1954, Katalog der Araneae, 2: 1289. Bonnet, 1958, Bibliographia Araneorum, 2: 3134. Tikader, 1962, J. Bombay Nat. Hist. Soc., 59: 683,

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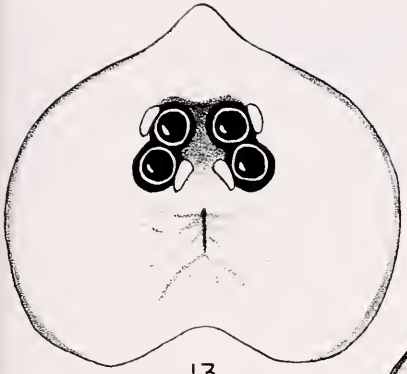
Dorsal views of corapoces. Figs. 13–20. 13. *Oecobius cellariorum*. 14. *O. annulipes*. 15. *O. concinnus*. 16. *O. interpellator*. 17. *O. putus*. 18. *O. isolatus*. 19. *O. isolatoides*. 20. *O. beatus*.



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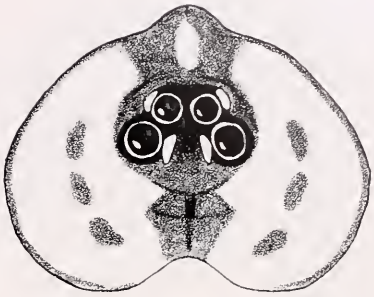

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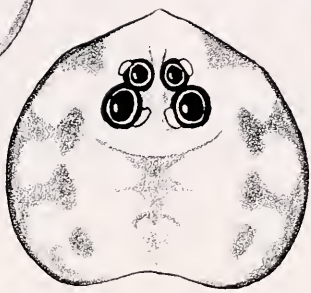

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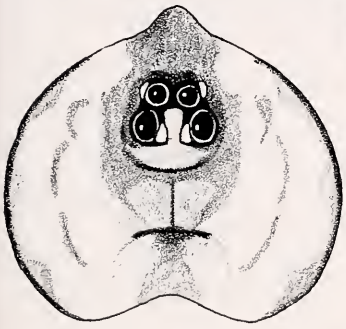

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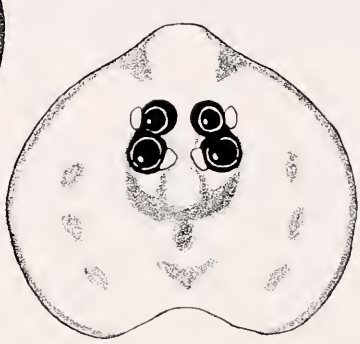

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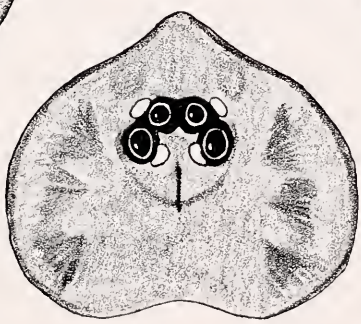

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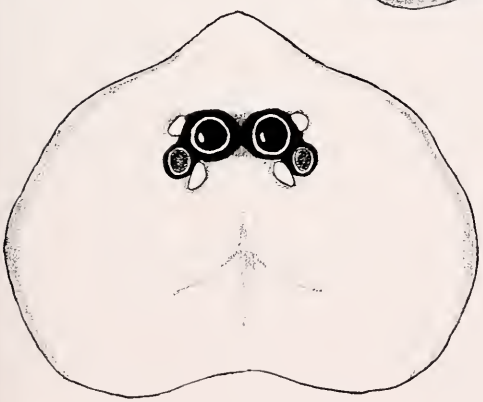

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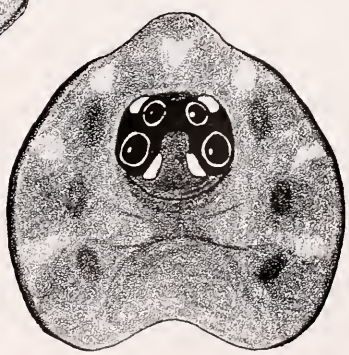

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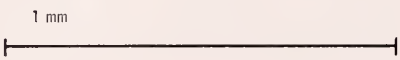


figs 1a–1d, ♂ ♀. Kritscher, 1966, Ann. Naturhist. Mus. Wien., 69: 290–291, pl. 1, fig. 11, pl. 2, fig. 12, ♂.
Ambika putus, Lehtinen, 1967, Ann. Zool. Fenn., 4: 433, fig. 32, ♀.

Diagnosis. Dinstinguished from all other Nearctic and Neotropical species of *Oecobius* by its large size, having the AME much the largest, and its lack of pattern.

Description. Female from Yuma, Arizona: carapace (Fig. 17) oval, wider than long (L/W = 1/1.2), with distinct shoulders on margin opposite eye region, clypeal projection evenly rounded. Carapace highest in eye area, sloping gradually and evenly in all directions. Thoracic groove transverse, indistinct. Eye area wider than long (L/W = 1/1.6), eyes in two transverse, slightly procurved lines. AME much the largest, separated by one diameter, ALE irregular, opalescent, separated from AME by their width. PLE slightly oval, one-half diameter of AME, separated from each other by nearly five times their diameter and from AME by their radius. PLE light, but not opalescent. PME irregular, subtriangular, opalescent, separated by nearly four times their width, almost contiguous with PLE. Spinnerets, cribellum, anal tubercle surrounded by a lightly sclerotized rim which bears a circle of long, incurved plumose hairs similar to those on anal tubercle. Legs with scattered hairs and few spines, spines irregularly arranged, but always present on ventrodistal portion of tibiae and metatarsi as pair of prolateral articular spines. Epigynum as in Figure 34. Remainder of structure as described for genus. Carapace off-white, unmarked except for black area around AME and PLE. Dusky marginal line faintly indicated, vague gray area around thoracic groove. Remainder of prosoma and legs off-white, unmarked. Abdomen pale gray, blotched chalky white. Venter pale gray, unmarked. Spinnerets and anal tubercle off-white. Total length, 3.15 mm. Carapace .94 mm long, 1.11 mm wide. Tibiae I–IV .91, 1.01, 1.01, 1.06 mm long, respectively. Metatarsi I–IV .86, 1.03, 1.12, 1.20 mm long, respectively.

Male from Yuma, Arizona, with structure essentially as in female, except as follows: carapace more nearly circular (L/W = 1/1.08), legs longer, thinner in proportion to body size. Calamistrum absent, cribellum suppressed. Body much more heavily clothed with plumose hairs, those on ridge around spinnerets much less obvious. Palpus as in Figures 56, 57. Coloration similar to that of female. Total length, 2.63 mm. Carapace 1.05 mm long, 1.13 mm wide. Tibiae I–IV .85, .86, .89, .97 mm long, respectively. Metatarsi I–IV .98, 1.00, .99, 1.10 mm long, respectively.

Ecological Notes. Mature males and females of this species were taken in January and February in Baja California, in April in Arizona and in May in Big Bend National Park, Texas. Mature specimens taken from June to August are represented from all these localities. At Tucson, Arizona, the species is common on the outsides of University buildings, with small webs stretched over "superficial inequalities," as Cambridge (1876) elegantly stated in the original description. Debski (1922) published more detailed reports on the ecology of this species and of *O. templi.* Only one collection places this spider away from buildings: a female was taken in a packrat nest near Sufford, Arizona.

Distribution. See Map 3. Southern California, southern Arizona, extreme westen New Mexico, southwestern Texas, northern Sonora and Chihuahua, and Baja California. Because of its synanthropic habits, this species is spread by man, and occurs throughout Africa (Paris Museum specimens fom Tanganyika examined by Ledoux) and India (Tikader, 1962).

Oecobius interpellator new species
Figures 16, 36, 58, 59; Pl. 1, Figures 1, 2

Holotype. Female from Cambridge, Massachusetts, Biological Laboratories, Harvard University, 20 February 1963, collected by J. A. Beatty, in the Museum

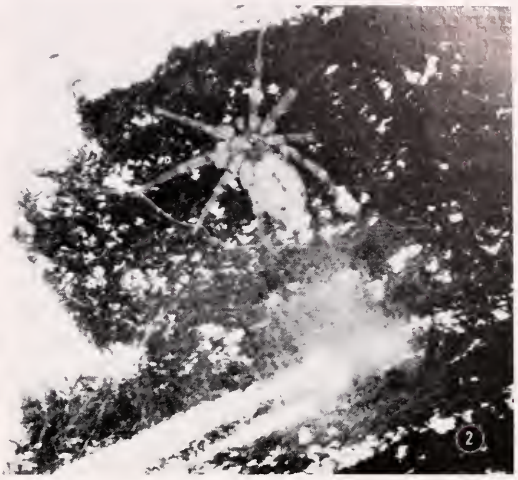


Plate I. Fig. 1. *Oecobius interpellator* female, dorsal view. Fig. 2. *O. interpellator* female and eggs in old web. The female later left the old web and built a new one in another part of the container.

of Comparative Zoology. Paratype male from the same locality in the Museum of Comparative Zoology. The specific epithet is a Latin noun in apposition, meaning invader, foreigner, or stranger.

Diagnosis. As a result of its limited distribution in the Nearctic region, this species is sympatric only with *O. annulipes*, to which it bears superficial resemblance. However, the epigynum of *O. interpellator* lacks a scape, and the palpus (Fig. 58) is distinct from that of *O. annulipes* in having a much larger conductor.

Description. Female from Cambridge, Massachusetts: carapace (Fig. 16) wider than long (L/W = 1/1.4), suboval, clypeal projection evenly rounded, almost squared off when seen from above. Eye area highest portion of carapace, carapace sloping evenly in all directions, slightly more abruptly to clypeus. Eyes in two nearly straight rows, PLE the largest, separated by slightly more than one diameter; PME irregular, opalescent, nearly contiguous with PLE, separated from each other by slightly less than their greatest width; PME round, dark, three-fourths as large as PLE and separated from PLE by a radius, from each other by one and one-fourth diameters; PLE oval, opalescent, nearly as large as PME, almost contiguous with PME. Epigynum (Fig. 36) of the *O. concinnus – O. beatus* pattern; copulatory openings anterior, separated by raised, wrinkled ridge resembling scape; ridge traversed medially by fertilization tubes, which turn abruptly laterad near posterior end of ridge, then curve back mesad and ventrad to open on either side of an oval depressed region limited anteriorly by blunt end of wrinkled ridge and posteriorly by transverse sclerotized rim. Internal genitalia fitting the *O. concinnus* pattern. Remainder of structure as described for genus. Coloration very similar to *O. annulipes;* carapace pale off-white with dusky marginal line; eyes ringed with black; vaguely indicated dusky area behind eyes extending in darker specimens to posterior margin of carapace, most specimens marked as shown in Figure 16; three submarginal dusky spots on each side. Abdomen unmarked with dusky areas, yellowish gray blotched chalky white. Sternum, coxae of legs and venter of abdomen off-white. Legs unmarked. The general impression is one of an intermediate between *O. annulipes* and *O. cellariorum.* Total length, 2.13 mm. Carapace .77 mm long, .88 mm wide. Tibiae I–IV .75, .71, .68, .79 mm long,

respectively. Metatarsi I–IV .68, .64, .65, .73 mm long, respectively.

Male from Cambridge, Massachusetts, with structure essentially as in female, except as follows: carapace somewhat rounder (L/W = 1/1.08); eye area wider in proportion to length than in female (L/W = 1/1.8); eyes smaller. Abdomen much smaller in proportion to carapace than in female. Calamistrum lacking from metatarsus IV. Palpal organ (Figs. 58, 59) of moderate size; radical apophysis absent; radix slightly produced at posterior lateral edge. Remainder of palpal structure close to *O. concinnus*. Coloration similar to female, but paler in most cases. Total length, 1.29 mm. Carapace .76 mm long, .82 mm wide. Tibiae I–IV .65, .71, .67, .73 mm long, respectively. Metatarsi I–IV .60, .65, .64, .72 mm long, respectively.

Ecological Notes. The mode of life of this species is very similar to that of *O. annulipes*. Despite extensive remodelling of the rooms in which it was originally collected, *O. interpellator* is still (September, 1968) remarkably common in the two rooms composing the insectary, and has spread to several adjacent rooms. All sizes except mature males were observed 20 September 1968, including six egg masses (Pl. 1, Fig. 2) left *in situ*, all containing four eggs. The collection from which the types were taken contained nearly forty mature males and females (February, 1963). Webs (Pl. 1, Fig. 1) cover virtually every corner and depression between cinder blocks, and are about a centimeter square, of the tubular type described by Glatz (1967). Debris in the webs consisted of tiny cockroach nymphs and small ants, all of which had been sucked dry without obvious damage to the cuticle. When prodded from their webs, the spiders run with great agility over the walls, but seem unable to cling to smooth, clean surfaces.

Distribution. Known only from the type locality. Presumably this species was imported with tropical cockroaches or ants. A sketch by Ledoux of a female in the British Museum (Natural History) from Noumea, New Caledonia, closely resembles this species.

Map 4. Southwestern North America, showing distribution of *O. isolatus* and *O. isolatoides*.

Oecobius isolatus Chamberlin
Figures 18, 35, 60, 61; Map 4

Oecobius isolatus Chamberlin, 1924, Proc. California Acad. Sci., 12: 584; immature holotype from Carmen Island, Gulf of California, in American Museum of Natural History, examined. Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 270, pl. 1, fig. 2, ♀. Roewer, 1954, Katalog der Araneae, 2: 1290. Bonnet, 1958, Bibliographia Araneorum, 2: 3133.

Oecobius parvus Chamberlin and Ivie, 1942, Bull. Univ. Utah, Biol. Ser., 32; 13; immature holotype from Virgin Narrows, near Littlefield, Arizona, in American Museum of Natural History, examined. Roewer, 1954, Katalog der Araneae, 2: 1290. NEW SYNONYMY.

Note. Both *O. isolatus* and *O. parvus* were described from immature specimens, a single example in the case of *O. parvus*

and two specimens of *O. isolatus*. Paratypes and holotypes of both were studied, and no structural differences in eyes and other features could be discerned. Only color and pattern differed, *O. parvus* resembling a very light *O. isolatus*.

The northernmost record of *O. isolatus* is in southwestern Yuma County, Arizona, and the southernmost for *O. parvus* is just over the Arizona-Utah border. But even in the absence of intermediate records, I am inclined to synonymize *O. parvus* under *O. isolatus*, since the only mature female available from the range of *O. parvus* has an epigynum identical to *O. isolatus*. Also, there is a distinct tendency for specimens of *O. isolatus* from the Baja peninsula to be somewhat darker than those from Arizona and California. If this trend is extrapolated, a light, *O. parvus*-like *O. isolatus* would be expected to occur in southern Utah. Additional collecting throughout extreme western Arizona is much to be desired.

Diagnosis. This species belongs to what might be termed the "Mexican group," a series of similar species (dark carapaces, broad epigynal scapes, palpi with large stipal and/or radical apophyses) obviously native to the region and not synanthropic. These species are best separated by reference to the figures, though *O. isolatus* is not sympatric with any of the others (Map 4). It is most closely related to *O. isolatoides*, but the palpus differs (Fig. 60), and the epigynal scape is not narrowed distally.

Description. Female from Fortuna Mine, Yuma County, Arizona: carapace (Fig. 18) subcircular, clypeal projection evenly rounded, more than one-fourth length of carapace, distinct shoulders at base of clypeal projection. Carapace nearly glabrous, with scattered plumose hairs. Eyes on distinct tubercle, sloping evenly to clypeus, but abruptly behind, then sloping gradually to posterior declivity. Posterior declivity sharp, limiting distinctly lower, lunate posterior area. Eyes in two rows, both moderately procurved. PLE the largest, separated from each other by two and one-half diameters; PME irregular, opalescent, separated from PLE by their width and from each other by their length. AME three-fourths diameter of PLE, separated from each other by one diameter and from PLE by one-half diameter of PLE. ALE irregular, opalescent, as large as AME, nearly contiguous with AME. Remainder of structure essentially as described for the genus. Epigynum (Fig. 35) large, with a broad scape, tracks of fertilization ducts visible in scape. Carapace entirely dark brown, eyes ringed with black, marginal line black, three lighter spots on each side just above marginal line. Coxae of legs, endites, labium pale yellow, sternum light brown. Abdomen blotched chalky dorsally, dark brown pattern near that described for *O. annulipes*. Venter pale, spinnerets and anal tubercle dark brown, surrounded by dark brown area. Legs with lateral maculae as follows: two maculae mesal and distal on all segments except patella and tarsi, patella wholly dark laterally, tarsi dark distally. Distal lateral maculae on tibiae and metatarsi forming complete or nearly complete rings. Total length, 2.40 mm. Carapace .87 mm long, .85 mm wide. Tibiae I–IV .68, .72, .65, .67 mm long, respectively. Metatarsi I–IV .65, .67, .68, .78 mm long, respectively.

Male from Roosevelt Dam, Yuma County, Arizona, with structure essentially as in female, except as follows: carapace flatter, broader in relation to width, much larger in comparison with abdomen. Eye area nearly twice as wide as long, eyes more dispersed. Coloration paler, but of the same pattern. Palpus (Figs. 60, 61) with a falcate apophysis on stipes and large, weakly sclerotized radical apophysis. Total length, 2.17 mm. Carapace .86 mm long, .98 mm wide. Tibiae I–IV .67, .68, .68, .76 mm long, respectively. Metatarsi I–IV .68, .74, .75, .82 mm long, respectively.

Ecological Notes. Nothing is known of this species' ecology.

Distribution. (Map 4) Lower Colorado Basin, Baja California.

Oecobius *isolatoides* new species
Figures 19, 37, 62, 63; Map 4

Holotype. Female from El Coyote, Sonora, 17.7 miles (28.3 kilometers) east of Rio Bavisbe and 48 miles (76.8 kilometers) east of Moctezuma, elev. 3200′, 12 July 1960, J. A. Beatty; paratype male from the same locality, in the American Museum of Natural History.

Diagnosis. The scape of the epigynum is nearly twice as long as wide, narrowed distally, and not folded; this combination of characters occurs in no other species of the "Mexican group." The male palpus resembles that of *O. isolatus*, but the radical apophysis of *O. isolatoides* is wider in proportion to its length, and not knobbed at the tip.

Description. Female from El Coyote, Sonora: carapace (Fig. 19) oval, wider than long (L/W = 1/1.1), clypeal projection evenly tapering from lateral margins, bluntly pointed. Carapace highest in eye area, sloping gently in all directions. Thoracic groove indistinct. Eye area wider than long (L/W = 1/1.7), eyes in two transverse, distinctly procurved rows. PLE the largest, separated by slightly more than two and one-half diameters. AME little more than half the diameter of PLE, separated from each other by one diameter and from PLE by a radius. PME opalescent, irregular-triangular, separated from each other by one and one-fourth their greatest width and from PLE by half their greatest width. ALE oval, opalescent, nearly as large as AME, separated from AME by their width. Epigynum (Fig. 37) with prominent scape, tapering to less than half its basal width, edges sigmoid. Fertilization tubes diverging at midlength, converging slightly near their openings. Remainder of structure as described for genus. Carapace nearly even medium tan, margins darker, submarginal dark shadings obsolete in some specimens. Eyes ringed with black. Remainder of coloration as described for *O. isolatus.* Total length, 2.04 mm. Carapace .77 mm long, .86 mm wide. Tibiae I–IV .56, .64, .59, .67 mm long, respectively. Metatarsi I–IV .56, .60, .60, .71 mm long, respectively.

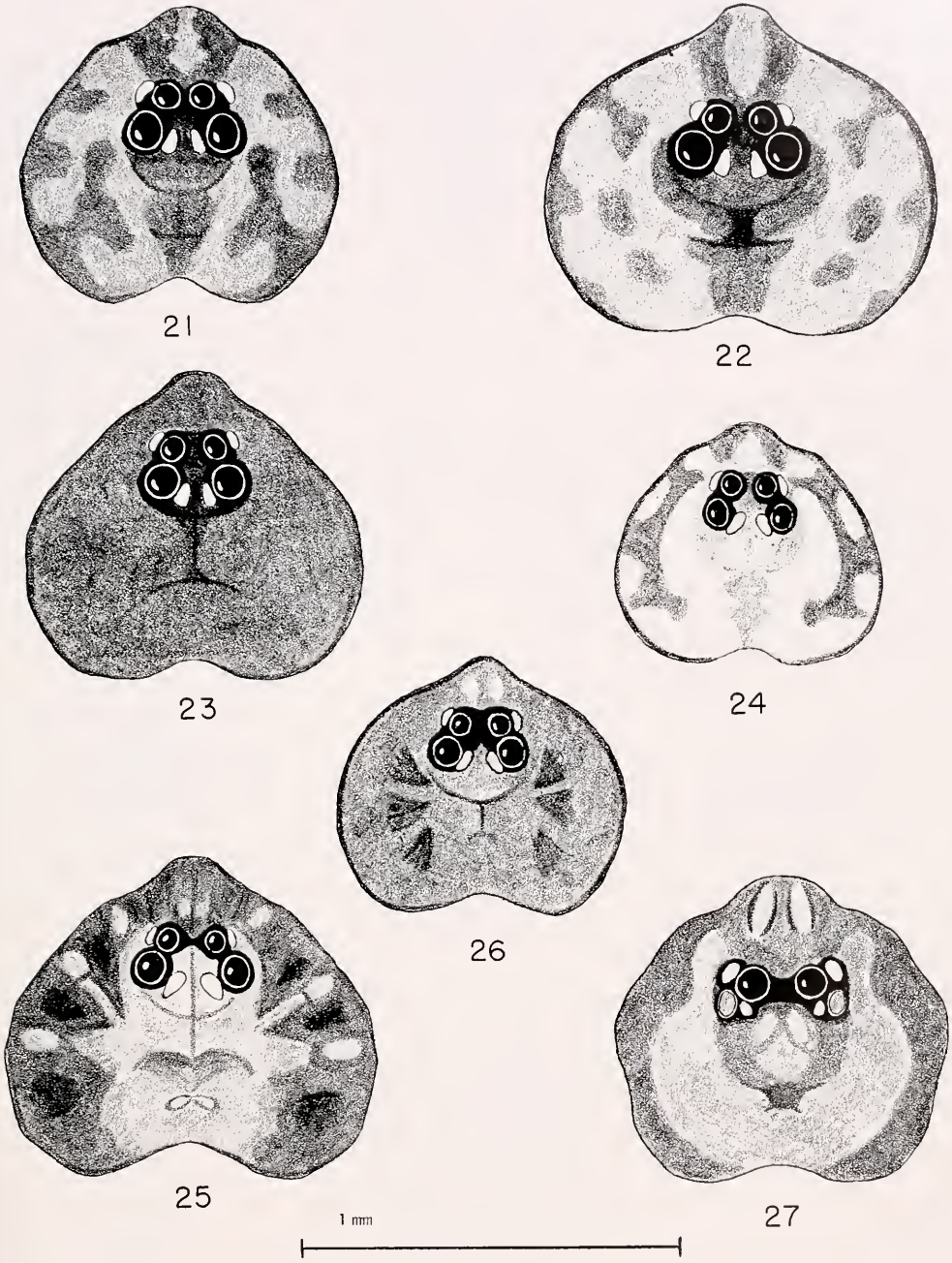
Male from El Coyote, Sonora, with structure essentially as in female, except as follows: carapace slightly flatter, wider in proportion to length (L/W = 1/1.12), eyes slightly smaller, more dispersed. Abdomen smaller in proportion to carapace, body generally more densely hairy. Sternum margined with specialized hairs. Coloration as described for female, but lighter in some specimens. Palpus (Figs. 62, 63) large, bulky. Radical apophysis blunt, gnarled, almost meeting process of stipes, which is smoothly curved and truncate. Conductor complex, intromittent portion of embolus concealed, visible only in direct ventral view as a short, heavily sclerotized curved spine. Total length, 1.82 mm. Carapace .75 mm long, .83 mm wide. Tibiae I–IV .56, .60, .57, .64 mm long, respectively. Metatarsi I–IV .53, .60, .59, .63 long, respectively.

Ecological Remarks. The Sonoran and Sinaloan localities are in desert thorn scrub. The type species were found under stones on a dry hillside. In Arizona, the species occurs in mountains, probably in the transition between Sonoran desert and woodland. Mature individuals have been collected in April, July, and August.

Distribution. (Map 4) Mountain foothills in Sonora, northern Sinaloa, and southern Arizona.

Oecobius *piaxtla* new species
Figures 21, 38, 64, 65

Holotype. Female from 20 miles (32 kilometers) west of Piaxtla, Sinaloa, 2 August 1964, W. J. Gertsch and J. Woods, collectors, in the American Museum of Natural History; male paratype from the same locality in the same museum. The specific name is a noun in apposition, after the type locality.



Dorsal views of carapaces. Figs. 21–27. 21. *Oecobius piaxtla*. 22. *O. rivula*. 23. *O. juangarcia*. 24. *O. bracae*. 25. *O. civitas*. 26. *O. culiacanensis*. 27. *Plataecobius floridanus*.

Diagnosis. Distinct from others of the "Mexican group" in details of the genitalia. The epigynal scape (Fig. 38) is as wide as long, and narrowed distally; the only species with a similar pattern is *O. civitas*, in which the scape is not narrowed distally. The male palpus (Figs. 64, 65) is somewhat smaller than the others bearing both stipal and radical apophyses.

Description. Female from 20 miles (32 kilometers) west of Piaxtla, Sinaloa: carapace (Fig. 21) subcircular (L/W = 1/1.12), clypeal projection low and rounded, shoulders at base of clypeal projection distinct. Carapace highest in eye area, sloping evenly in all directions; thoracic groove transverse, poorly indicated. Eyes in two slightly procurved rows; eye area nearly half again as wide as long (L/W = 1/1.35). PLE the largest, separated by nearly two diameters; PME irregular, opalescent, separated from each other by their greatest width, nearly contiguous with PLE. AME two-thirds diameter of PLE, separated from each other by slightly more than one radius, nearly contiguous with PLE; ALE irregular, opalescent, nearly contiguous with AME. Epigynum (Fig. 38) with scape as wide or slightly wider than long, traversed by fertilization ducts. Internal genitalia of the *O. civitas* pattern, but copulatory ducts open almost immediately into spermathecae. Remainder of structure as described for genus. Carapace with light brown ground color, overlaid with dark brown pattern as in Figure 21. Eyes ringed with black, eye tubercle dark brown to black; clypeus light mesally, with two parallel dark bands laterally; marginal line black, with dark brown areas extending into submarginal region as figured; dark brown band extending from eye tubercle to posterior margin of carapace. Labium light brown, sternum light brown, margined dark brown. Leg annulations of the typical pattern; all incomplete. Total length, 2.82 mm. Carapace .77 mm long, .83 mm wide. Tibiae I–IV .48, .49, .48, .56 mm long, respectively. Metatarsi I–IV .45, .49, .47, .54 mm long, respectively.

Male from 20 miles (32 kilometers) west of Piaxtla, Sinaloa, with structure essentially as in female, except as follows: carapace wider in proportion to length, eyes smaller, more dispersed than in female. Carapace with two lunate submarginal depressions, presumably serving for muscle attachment for palpus. Palpus (Figs. 64, 65) large, tegular apophysis complex, nearly trifid; conductor broadly spatulate, embolus with all the usual processes well developed and large. Coloration as in female, somewhat lighter. Total length, 2.00 mm. Carapace .80 mm long, .90 mm wide. Tibiae I–IV .53, .59, .56, .62 mm long, respectively. Metatarsi I–IV .51, .56, .58, .64 mm long, respectively.

Ecological Notes. Found under rocks in desert thorn scrub.

Distribution. Known only from the type locality.

Oecobius rivula new species
Figures 7, 8, 22, 39, 68, 69

Holotype. Female from 32 miles (51.2 kilometers) east of Villa Union, Sinaloa, 26 August 1965, collected by W. J. Gertsch and J. Hastings; paratype male from the same locality, in the American Museum of Natural History. The specific epithet is a noun in apposition, Latin for crevice.

Diagnosis. Easily distinguished from all others of the "Mexican group" by the folded epigynal scape with a perforation at the tip (Fig. 39), and by the extraordinarily massive male palpus with an elongate cluster of small knobs on the inner side of the radical apophysis (Fig. 69).

Description. Female from 32 miles (51.2 kilometers) east of Villa Union, Sinaloa: carapace (Fig. 22) suboval, wider than long (L/W = 1/1.16), clypeal projection evenly rounded, shoulders lacking at base of clypeus. Carapace highest in eye region, sloping gradually in all directions, somewhat more steeply to clypeus. Eye area

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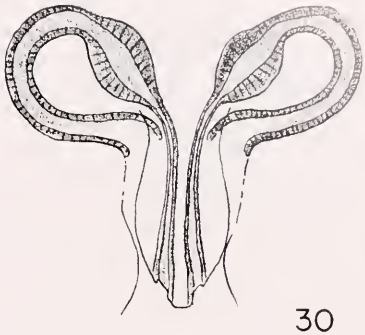

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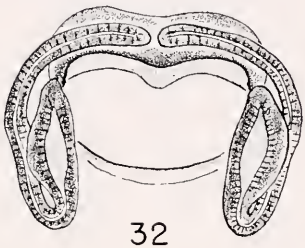

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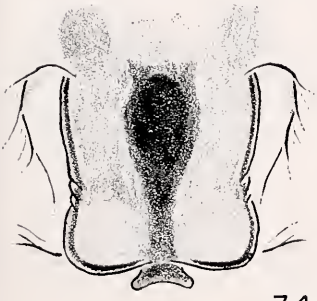

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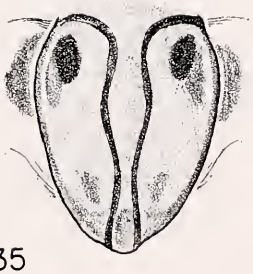

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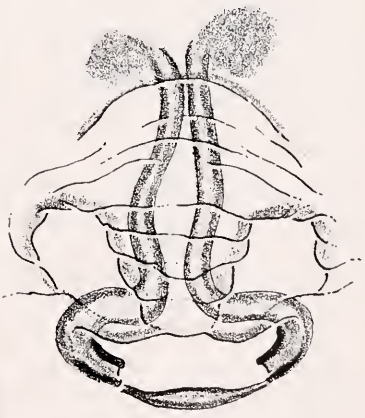

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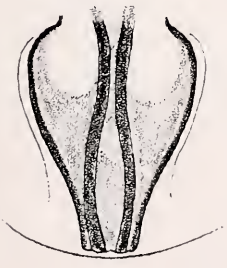

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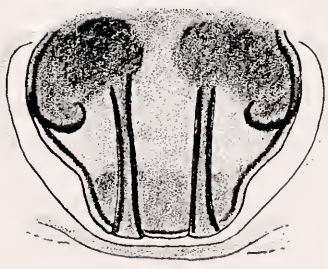

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emale epigyna. Figs. 28–38. 28. *Oecobius cellariarum*, ventral view. 29. *O. annulipes*, ventral view. 30. *O. annulipes*, larsal view. 31. *O. concinnus*, ventral view. 32. *O. concinnus*, dorsal view. 33. *O. beatus*, ventral view. 34. *O. putus*, entral view. 35. *O. isalatus*, ventral view. 36. *O. interpellatar*, ventral view. 37. *O. isolataides*, ventral view. 38. *O. iaxtla*, ventral view.

wider than long (L/W = 1/1.88); eyes in two slightly procurved rows. PLE much the largest, separated from each other by two and one-quarter diameters; PME irregular, opalescent, separated from each other by one and one-quarter their greatest width, from PLE by one-half their greatest width; AME two-thirds diameter of PLE, separated from each other by slightly less than one diameter, from PLE by less than a radius; ALE irregular, opalescent, nearly contiguous with AME. Epigynum (Fig. 39) large, well-defined, lying in depression that is longer than wide. Scape long, folded anteriorly, then posteriorly, most anterior portion when seen in ventral view broadly rounded, tapering to less than half its width. Fertilization ducts clearly visible in scape; tip of scape with small, round perforation. Remainder of structure typical for genus. Ground color of carapace light brown, eyes ringed with black; central dark brown band forked anterior to eyes, central part of clypeus light. Marginal band dark brown, widened opposite coxae of legs. Submarginal spots in some cases connected to marginal band. Sternum, labium, and venter light, as described for *O. isolatus*. Leg annulations incomplete, as described for *O. isolatus*. Total length, 3.05 mm. Carapace .92 mm long, 1.05 mm wide. Tibiae I–IV .76, .76, .75, .80 mm long, respectively. Metatarsi I–IV .75, .75, .75, .83 mm long, respectively.

Male from 32 miles (51.2 kilometers) east of Villa Union, Sinaloa, with structure essentially as in female except as follows: carapace slightly longer in proportion to width (L/W = 1/1.08); eyes smaller more dispersed than in female. Carapace with two deep submarginal lunate depressions, possibly associated with muscle attachments for massive palpi. Remainder of structure as described for genus. Palpus (Figs. 68, 69) unusually large, massive; radical apophysis forked apically, coarsely rugose on mesal edge; hooks of conductor close together; stipal hook large, as long as cymbium, spatulate distally. Coloration as described for female, somewhat lighter. Total length, 2.34 mm. Carapace 1.05 mm long, 1.14 mm wide. Tibiae I–IV .70, .75, .71, .79 mm long, respectively. Metatarsi I–IV .70, .71, .70, .80 mm long, respectively.

Ecological Notes. The specimens were collected at the type locality from a deep, wet crevice.

Distribution. This species is known only from the type locality.

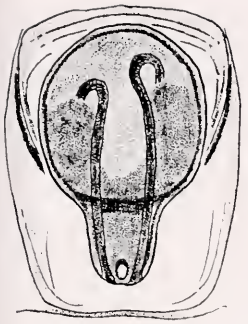
Oecobius juangarcia new species

Figures 23, 40, 66, 67

Holotype. Female from Juan Garcia, Oaxaca, 1 September 1964, collected by J. and W. Ivie; male paratype from same locality, both in American Museum of Natural History. The specific name is a noun in apposition, after the type locality.

Diagnosis. Distinct from others of the "Mexican group" in the centrally depressed epigynal scape (Fig. 40), and the less complex palpus (Figs. 66, 67) which lack a radical apophysis. A radical apophysis is lacking in *O. civitas* also, but the general appearance of the palpus is quite different, particularly in the conductor.

Description. Female from Juan Garcia, Oaxaca: carapace (Fig. 23) suboval (L/W = 1/1.3), clypeal projection indistinct, rounded, shoulders at base of clypeal projection poorly developed. Carapace with scattered plumose white hairs. Eyes on low tubercle, sloping evenly in all directions to margin of carapace; thoracic furrow indistinct. Eyes in two slightly procurved rows; eye area wider than long (L/W = 1/1.28). PLE the largest, separated from each other by slightly more than one diameter; PME irregular, opalescent, nearly contiguous with PLE, separated from each other by their greatest width. AME two-thirds diameter of PLE, narrowly separated from PLE; separated from each other by slightly more than one diameter; ALE irregular, opalescent, nearly contiguous with AME. Epigynum (Fig. 40) as wide as long, somewhat reniform; scape margined, perforated anteriorly with



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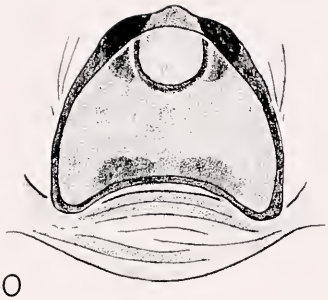

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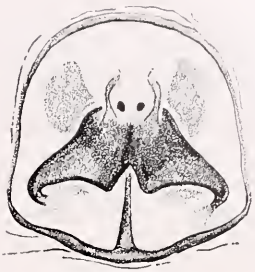

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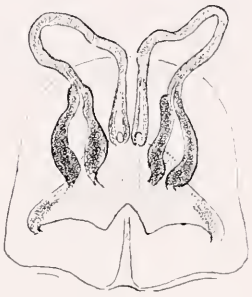

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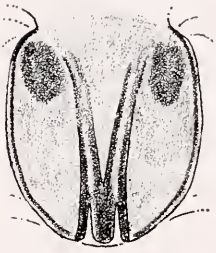

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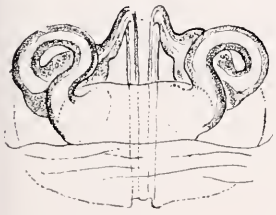

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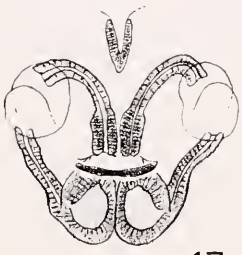

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Female epigyna. Figs. 39–47. 39. *Oecobius rivula*, ventral view. 40. *O. juangarcia*, ventral view. 41. *O. bracae*, ventral view. 42. *O. bracae*, dorsal view. 43. *O. civitas*, ventral view. 44. *O. civitas*, dorsal view. 45. *O. culiacanensis*, ventral view. 46. *Platoecobius floridanus*, ventral view. 47. *P. floridanus*, dorsal view.

a large fossa. Internal genitalia not examined on only available female specimen, but presumably similar to *O. rivula*. Remainder of structure as described for genus. Carapace entirely medium brown, eyes ringed with black, eye area dark brown. Coxae of legs, endites, pale yellow, labium and sternum medium brown. Abdomen blotched chalky dorsally, with typical pattern of dark brown areas; venter mostly pale. Legs annulated and blotched as described for *O. isolatus*. Total length, 2.56 mm. Carapace .80 mm long, .91 mm wide. Tibiae I–IV .52, .53, .51, .57 mm long, respectively. Metatarsi I–IV .50, .50, .49, .59 mm long, respectively.

Male from Juan Garcia, Oaxaca, with structure essentially as in female except as follows: carapace wider in proportion to length (L/W = 1/1.22); eyes smaller, more dispersed, eye area wider in proportion to length than female (L/W = 1/1.4). Cara-

pace with two submarginal lunate depressed areas, presumably serving as points of muscle attachment for palpi. Palpus (Figs. 66, 67) strongly modified from basic form described for *O. isolatus*, distal portion of stipes greatly lengthened and curved around face of radix; intromittent portion emerging from behind conductor ventromesally; conductor reduced, radical apophysis absent. Total length, 2.01 mm. Carapace .76 mm long, .93 mm wide. Tibiae I–IV .48, .49, .46, .52 mm long, respectively. Metatarsi I–IV .49, .51, .46, .60 mm long, respectively.

Ecological Notes. Little is known of the ecology of this species. A male from near Tehuantepec, Oaxaca, was taken from a small web between the ribs of a cereoid cactus.

Distribution. Central Oaxaca.

Oecobius bracae new species

Figures 24, 41, 42, 70, 71

Holotype. Female from three miles (4.8 kilometers) west of Tehuantepec, Oaxaca, 28 April 1963, collected by W. J. Gertsch and W. Ivie; paratype male from the same locality, both in the American Museum of Natural History. The specific epithet is a Latin noun in apposition, "a short, pants-like garment," and is derived from the unusual form of the epigynum.

Diagnosis. The color pattern distinguishes this species from all others in the "Mexican group," but could lead to confusion with *O. beatus*. The epigynal scape is highly distinctive in both species; in *O. bracae* (Fig. 41) the fertilization tubes open flush with the surface, in *O. beatus* (Fig. 33) they open on the tips of short projections. The palpus of *O. bracae* (Fig. 71) has a much smaller stipes than that of *O. beatus* (Fig. 55).

Description. Female from three miles (4.8 kilometers) west of Tehuantepec, Oaxaca: carapace (Fig. 23) nearly rounded (L/W = 1/1.03), clypeal projection blunt, clypeal shoulders fairly distinct. Carapace evenly domed at eye area, sloping almost at an equal angle in all directions. Eyes in two rows, first row nearly straight, second perceptibly procurved. Eye area wider than long (L/W = 1/1.5). PLE the largest, separated by twice their diameter; PME irregular, opalescent, nearly contiguous with PLE, separated from each other by slightly less than their greatest width. AME nearly three-fourths diameter of PLE, separated from each other by a little less than their diameter and from PLE by their radius; ALE opalescent, irregular, nearly contiguous with AME. Female epigynum very distinctive, consisting of a deep, semi-rectangular depression in which prominent, flared openings of vulvae are situated (Fig. 41). Anteriorly, fertilization tubes open into a shallow, rimmed depression. Internally (Fig. 42), a single pair of spermathecae open almost directly to outside, fertilization tubes curve far anteriorly just under cuticle until they loop back to open as described above. Remainder of structure typical for genus. Carapace off-white, eyes ringed black which separates them into two lateral groups, eye tubercle covered by extensive dusky area interrupted by two symmetrical light areas immediately behind eyes, and extending as irregular band to posterior margin of carapace. Submarginal band dark brown, connected with brownish black marginal line just behind clypeal shoulders and at two other points evenly spaced posteriorly. Clypeus dark brown, with central white area. Abdomen pale gray, blotched chalky, cardiac mark brown. Legs banded as follows: incomplete median and distal bands on femur, tibia and metatarsus; patella with a single, distal band, incomplete dorsally. Tarsus somewhat darker distally. Remainder of coloration as described for *O. beatus*. Total length, 1.96 mm. Carapace .63 mm long, .65 mm wide. Tibiae I–IV .38, .38, .40, .48 mm long, respectively. Metatarsi I–IV .39, .42, .41, .50 mm long, respectively.

Male from three miles (4.8 kilometers) west of Tehuantepec, Oaxaca, with struc-

ture essentially as in female except as follows: carapace somewhat wider in relation to length (L/W = 1/1.1), eye group more compact (L/W = 1/.96). Legs longer in proportion to body, body more densely hairy. Coloration as in female, carapace of some specimens more lightly marked. Papal organ (Figs. 66, 67) of the moderately large type, as figured. Total length not known, abdomen missing on all mature male specimens. Carapace .55 mm long, .61 mm wide. Tibiae I–IV .34, .35, .33, .43 mm long, respectively. Metatarsi I–IV .36, .37, .37, .45 mm long, respectively.

Ecological Notes. Nothing is known of the ecology of this species.

Distribution. Central Oaxaca.

Oecobius civitas new species

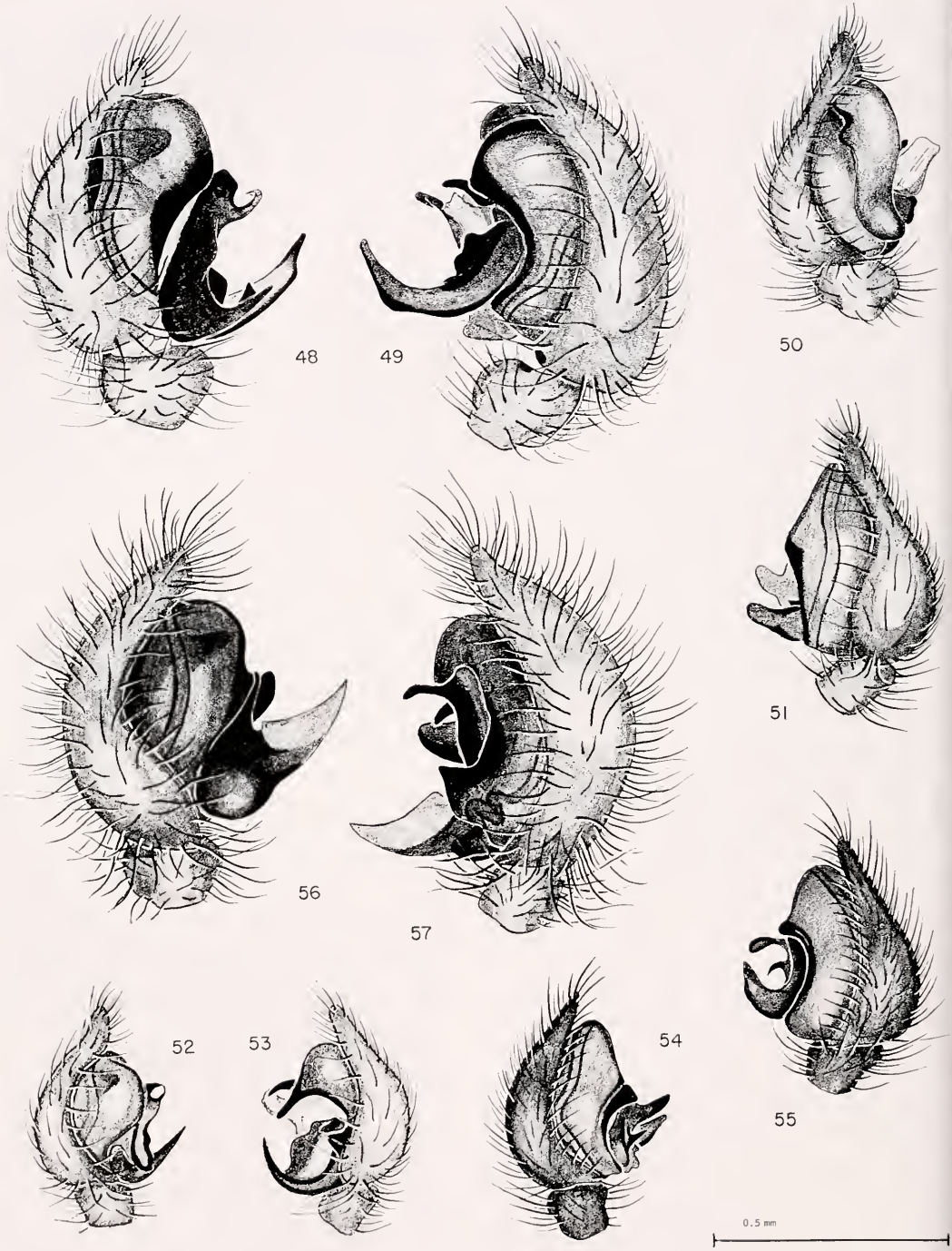
Figures 25, 43, 44, 72, 73; Map 3

Holotype. Female from west side of Lake Sayula, Jalisco, 30 July 1964, collected by W. J. Gertsch and J. Woods; paratype male from the same locality, both in the American Museum of Natural History. The specific epithet is a Latin noun in apposition, "community," and is derived from the evident communal existence of the species.

Diagnosis. Resembles *O. culiacanensis* in having the epigynal scape as wide as long, but the scape of *O. civitas* is not narrowed distally (Fig. 43). The palpus is distinct from all others of the "Mexican group," lacking both a radical apophysis and a large stipal process (Figs. 72, 73).

Description. Female from Lake Sayula, Jalisco: carapace (Fig. 28) suboval, wider than long (L/W = 1/1.2), clypeal projection evenly rounded, shoulders at base of clypeus indistinct. Carapace highest in eye region, sloping gradually behind and abruptly to clypeus, fairly heavily clothed with white plumose hairs, otherwise glabrous. Eye area wider than long, (L/W = 1/1.7), eyes in two slightly procurved rows. PLE much the largest, separated by two and one-half times their diameter, round, dark. PME irregular, opalescent, twice as long as wide, separated from each other by their greatest width and from PLE by two-thirds their greatest width. AME round, dark, nearly one-half diameter of PLE, separated from each other by twice their diameter, from PLE by one diameter. ALE irregular, opalescent, separated from AME by slightly more than one radius of AME. Epigynum as in Figures 43, 44. Remainder of structure as described for genus. Carapace with ground color of dark grayish tan, irregularly mottled dark brown, eyes ringed with black. Clypeus dark brown, margins of carapace dark brown with three lighter areas opposite legs I, II, and III. Central band of carapace grayish tan, procurved darker arc at thoracic groove, two recurved darker arcs behind, the last surrounding lighter "spectacle-like" area. Sternum, labium, coxae of legs tan ventrally. Abdomen dark brown ventrally, laterally, and in cardiac area with two light tan stripes paralleling cardiac area, large light tan macula over anal tubercle. Spinnerets and anal tubercle brown. Legs tan, all with a similar pattern of maculae and bands: coxae banded dark brown distally, femora with median band incomplete dorsoposteriorly, distal annulus complete; patellae dark brown proximally and dorsally; median annulus on tibiae complete, distal annulus complete except for narrow posterior band; median and distal annuli of metatarsi complete; tarsi shaded dark brown distally. Total length, 1.97 mm. Carapace .82 mm long, .98 mm wide. Tibiae I–IV .62, .69, .66, .75 mm long, respectively. Metatarsi I–IV .60, .66, .72, .80 mm long, respectively.

Male from Lake Sayula, Jalisco, with structure essentially as in female, except as follows: carapace wider in proportion to length (L/W = 1/1.3), eyes somewhat more dispersed, carapace more heavily clothed with procumbent white plumose hairs, abdomen smaller in relation to carapace. Calamistrum absent from leg IV. Coloration similar to female, somewhat lighter. Palpus as in Figures 72, 73. Total



Male right palpi. Figs. 48–57. 48. *Oecobius cellariarum*, lateral view. 49. *O. cellariarum*, mesal view. 50. *O. annulipes*, lateral view. 51. *O. annulipes*, mesal view. 52. *O. cancinnus*, lateral view. 53. *O. cancinnus*, mesal view. 54. *O. beatus*, lateral view. 55. *O. beatus*, mesal view. 56. *O. putus*, lateral view. 57. *O. putus*, mesal view.

length, 1.72 mm. Carapace .72 mm long, .95 mm wide. Tibiae I–IV .60, .66, .66, .75 mm long, respectively. Metatarsi I–IV .60, .68, .68, .76 mm long, respectively.

Ecological Notes. Communities of these medium-sized oecobiids weave large webs on the undersides of rocks on the shores of Lake Sayula, Jalisco. Intact whole webs were collected in July, 1964, by Willis J. Gertsch and J. Woods and deposited in the American Museum of Natural History. Each web contained between 60 and 140 individuals of approximately the same age, in most cases in the penultimate instar, with a few adults. Each individual seemed to have its own pocket or retreat in the communal web. Large egg sacs were found near the centers of two of the webs, each containing nearly 200 deutova clearly identifiable as oecobiids; in both these cases, most of the previous (?) generation were in the penultimate instar. Numerous insect parts were found tangled in the webs, mostly from ants, small beetles, and from thysanurans. The vials containing the webs also contained numerous spiders of the families Pholcidae, Filistatidae, Ganphosidae, Oonopidae, and Scytotidae. The relationship of these spiders to the oecobiids is not known; perhaps they were merely collected at the same time.

Distribution. (Map 3) Jalisco, Morelos, Guerrero, Oaxaca.

Oecobius culiacanensis new species

Figures 26, 45, 74, 75

Holotype. Female from six miles (9.6 kilometers) south of Culiacan, Sinaloa, 22 July 1954, collected by W. J. Gertsch; male paratype from the same locality, both in the American Museum of Natural History. The specific epithet is formed from the name of the type locality: "of Culiacan."

Diagnosis. Females may be distinguished from other members of the "Mexican group" by the epigynal scape, which is longer than wide, not folded, and bears two distal notches (Fig. 45). The stipal process of the male palpus is more spatulate than in any other species (Figs. 74, 75).

Description. Female from six miles (9.6 kilometers) south of Culiacan, Sinaloa: carapace (Fig. 26) wider than long (L/W = 1/1.12), suboval, clypeal projection slightly pointed. Eye area highest region of carapace, sloping evenly in all directions, slightly more gradually posteriorly. Eye area wider than long (L/W = .74/1), eyes in two slightly procurved rows. PLE dark, the largest, separated from each other by one and one-fourth their diameter; PME irregular, opalescent, nearly contiguous with PLE, separated from each other by their greatest width; AME dark, slightly more than one-half diameter of PLE, separated from PLE by a radius, from each other by one and one-half diameters; ALE opalescent, irregular, nearly contiguous with AME. Epigynum (Fig. 45) of the *O. civitas* type, with a broad oval scape traversed mesally by fertilization ducts, posterior margin deeply notched; fertilization ducts opening into notches. Internal genitalia typical. Remainder of structure as described for genus. Carapace evenly dusky brown-black, eyes ringed with black, submarginal markings in three series, slightly darker. Clypeus with two pale spots. Abdomen marked with dark blotches and chalky patches as described for *O. isolatus.* Sternum pale, margined heavily posteriorly with brown. Remainder of color as described for *O. civitas*, but leg bands on tibiae and metatarsi in the form of complete annuli. Total length, 2.20 mm. Carapace .66 mm long, .76 mm wide. Tibiae I–IV .55, .60, .55, .64 mm long, respectively. Metatarsi I–IV .54, .58, .55, .67 mm long, respectively.

Male from six miles (9.6 kilometers) south of Culiacan, Sinaloa, with structure essentially as in female, except as follows: carapace with two submarginal crescentic depressions running from eye area to thoracic furrow, presumably acting to provide muscle attachments for the large palpi. Palpus (Figs. 74, 75) massive, radical

Male right palpi. Figs. 58–67. 58. *Oecobius interpellatar*, lateral view. 59. *O. interpellatar*, mesal view. 60. *O. isolatus*, lateral view. 61. *O. isolatus*, mesal view. 62. *O. isolataides*, lateral view. 63. *O. isolataides*, mesal view. 64. *O. piaxtla*, lateral view. 65. *O. piaxtla*, mesal view. 66. *O. juangarcia*, lateral view. 67. *O. juangarcia*, mesal view.

apophysis blunt, stipes large, cupped, terminating in spatulate point. Conductor complex. Coloration as in female, somewhat lighter. Total length 1.86 mm. Carapace .82 mm wide, .72 mm long. Tibiae I–IV .47, .50, .50, .53 mm long, respectively. Metatarsi I–IV .45, .50, .46, .59 mm long, respectively.

Ecological Notes. All the known localities for this species are in subtropical thorn scrub.

Distribution. Southern and western Sinaloa.

Genus *Platoecobius* Chamberlin and Ivie, 1935

Platoecobius Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 270; type species by original designation and monotypy *Platoecobius floridanus* (Banks); Lehtinen, 1967, Ann. Zool. Fenn., 4: 259, 304.

Diagnosis. Separated from *Oecobius*, the only other genus in the family, by the shorter, stouter legs, the calamistrum extending the entire length of metatarsus IV, and the simpler genitalia.

Description. Small oecobiid spiders (2–3 mm total length), with the characters of the family. Carapace with sides slightly sinuate, clypeus broad, evenly rounded. Carapace flat, head region slightly elevated. Eyes on low tubercle, eye area much wider than long. AME round, dark; PLE round, dark, but lighter in color than AME; PLE and ALE light and irregular in shape. Macrosetae of eye area as follows: one immediately behind each AME and PLE; two behind eye area at posterior declivity, separated by more than the diameter of AME. Thoracic groove very indistinct, transverse. Carapace slightly depressed above pedicel. Abdomen flattened, almost elongate-pentagonal. Legs stout, spines entirely lacking. Tarsi and metatarsi without trichobothria. Hind coxae separated by sternum. Calamistrum lacking in mature males, extending in immature specimens and females along entire length of metatarsus IV. Palpi of mature males with tegulum lacking, radix spiral, making more than one turn, conductor small, membranous. Females without elaborate epigynal modification, two pair of spermathecae, one heavily sclerotized, the other saclike.

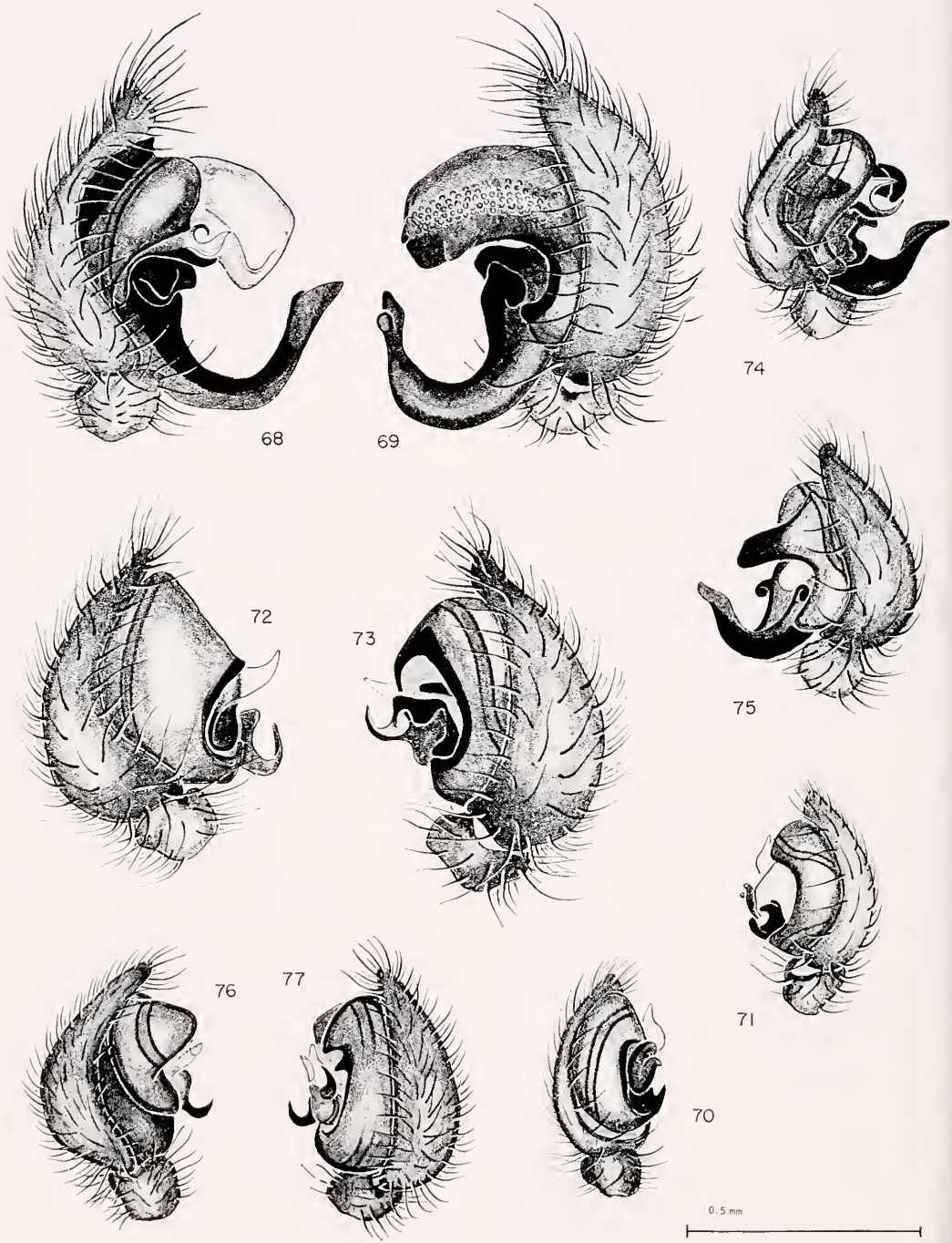
Platoecobius floridanus (Banks)

Figures 27, 46, 47, 76, 77; Map 2

Thalamia floridanus Banks, 1893, Trans. Amer. Entomol. Soc., 23: 58; holotype ♀ from Lake Worth, Florida, in American Museum of Natural History, examined.

Platoecobius floridanus, Chamberlin and Ivie, 1935, Ann. Entomol. Soc. Amer., 28: 270, pl. 4, figs. 22–32, ♀. Roewer, 1954, Katalog der Araneae, 2: 1290; Bonnet, 1958, Bibliographia Araneorum, 2: 3699.

Description. Female from Highlands Hammock State Park, Florida: carapace (Fig. 27) suboval, slightly wider than long (L/W = 1/1.08), widest just posterior to eyes, edge slightly undulate, clypeal projection broad, evenly rounded. Carapace highest in eye area, elevation prolonged somewhat behind eyes, sloping evenly in all directions. Thoracic groove very indistinct. Eye area wider than long (L/W = 1/2.25), eyes in two rows, the first slightly procurved, the second straight. AME the largest, separated by one diameter, dark. ALE opalescent, subequal in size to AME, slightly irregular, nearly contiguous with AME, their posterior edges lying on a line through centers of AME. PLE light, but not opalescent, separated from each other by nearly six times their diameter, nearly contiguous with AME. PME nearly one-half the diameter of PLE, slightly irregular, opalescent, nearly contiguous with PLE. The general impression is one of two well-separated tetrads of eyes. Legs proportionally stouter than in any *Oecobius* species. Epigynum as in Figures 46, 47. Remainder of structure as described for the genus. Ground color medium tan. Carapace with darker marginal bands, eyes surrounded by black, clypeal projection with two parallel light stripes set off by darker lines on each side.



Male right palpi. Figs. 68–77. 68. *Oecobius rivula*, lateral view. 69. *O. rivula*, mesal view. 70. *O. bracae*, lateral view. 71. *O. bracae*, mesal view. 72. *O. civitas*, lateral view. 73. *O. civitas*, mesal view. 74. *O. culiacanensis*, lateral view. 75. *O. culiacanensis*, mesal view. 76. *Platoecobius floridanus*, lateral view. 77. *Platoecobius floridanus*, mesal view.

Thoracic groove slightly darker. Abdomen pale dorsally, dark brown on sides. Venter nearly white, spinnerets and anal tubercle dark brown dorsally. Sternum, coxae of legs, labium nearly white. Legs irregularly blotched darker, blotching very indistinct on most specimens. Total length, 2.40 mm. Carapace .82 mm long, .88 mm wide. Tibiae I–IV .52, .52, .48, .54 mm long, respectively. Metatarsi I–IV .38, .44, .38, .49 mm long, respectively.

Male from Highlands Hammock, Florida, with structure essentially as in female, except as follows: carapace somewhat wider in proportion to length (L/W = 1/1.1), eye area not so wide in proportion to its length (L/W = 1/1.9). Proportions of eyes as in female. Calamistrum absent, cribellum suppressed. Body much more heavily clothed with hairs. Palpus as in Figures 76, 77. Coloration similar to female, somewhat lighter. Total length, 2.02 mm. Carapace .75 mm long, .82 mm wide. Tibiae I–IV .49, .49, .45, .47 mm long, respectively. Metatarsi I–IV .36, .38, .38, .44 mm long, respectively.

Ecological Notes. Chamberlin and Ivie (1935) record this species as being found beneath the bark of trees, and note that no prey-catching web has been observed. They did not remark on retreats that may have been built by the spider. It is possible that the enlarged, forward-directed median eyes are an adaptation to a vagrant, hunting existence. Mature representatives of both sexes have been taken in December, February, and August.

Distribution. (Map 2) Central Florida, inland Georgia, and South Carolina.

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(Received 28 November 1968.)

INDEX

Valid names are in italics; only major discussions cited.

Ambika, 134, 135
annulipes, *Oecobius*, 138
audanti, Oecobius, 141

beatus, *Oecobius*, 143
beatus, Oecobius, status of "allotype male," 141
benneri, Oecobius, 141
bracae, *Oecobius*, 156

cellariorum, Clotho, 136
cellariorum, *Oecobius*, 136
civitas, *Oecobius*, 157
concinnus, *Oecobius*, 141
culiacanensis, *Oecobius*, 159

domesticus, Oecobius, 137

floridanus, *Platoecobius*, 161
floridanus, Thalamia, 161

interpellator, *Oecobius*, 146
isolatoides, *Oecobius*, 150
isolatus, *Oecobius*, 148

juangarcia, *Oecobius*, 154

Maitreja, 134
marathaus, *Maitreja*, 134

nieborowskii, Oecobius, 141
nieborowskii, Tarapaca, 141
nieborowskii, Thalamia, 141

Oecobius, 135
Omanus, 135

parietalis, Oecobius, 138
parietalis, Thalamia, 138
parvus, Oecobius, 148
piaxtla, *Oecobius*, 150
Platoecobius, 161
putus, Ambika, 146
putus, *Oecobius*, 144

rivula, *Oecobius*, 152

sapporensis, "Oecobius," 131

Tarapaca, 134, 135
templi, *Oecobius*, observed by Debski, 129, 146
texanus, Oecobius, 137
Thalamia, 134, 135

Uroctea, 130

vokesi, Oecobius, 141

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Systematics and Biology of The Stromateid Fishes of the Genus *Peprilus*

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SYSTEMATICS AND BIOLOGY OF THE STROMATEID FISHES OF THE GENUS *PEPRILUS*[1]

MICHAEL H. HORN[2]

TABLE OF CONTENTS

Abstract 165
Introduction 166
Materials and Methods 169
Systematics 170
Genus *Peprilus* 170
Key to the Species of *Peprilus* 173
Peprilus medius 175
Peprilus ovatus 182
Peprilus simillimus 185
Peprilus snyderi 189
Peprilus burti 192
Peprilus triacanthus 197
Peprilus paru 202
Aspects of Functional Morphology 210
Aspects of Life History and Ecology 220
Evolutionary Relationships and Zoogeography 239
Acknowledgments 252
Summary 254
Literature Cited 255

ABSTRACT

A complete revision is presented of the genus *Peprilus*, one of the three genera of the family Stromateidae. The nominal genera *Poronotus* and *Palometa* are placed in the synonymy of *Peprilus*. Seven species are recognized, and one, *Peprilus ovatus* from the northern Gulf of California, is newly described.

Several aspects of functional morphology are considered. The vertebral column, skull, and pectoral fins appear to ossify earlier than the caudal skeleton and median fins, a sequence interpreted as being correlated with an early planktonic life followed by an independent nektonic existence. Vertebral number is relatively constant within a species and is considered to be of possible selective value in maintaining a certain body form. The absence of pelvic fins, the long pectoral fins which are used extensively for propulsion in adult fishes, and the compressed body, may all be correlated with the continuous swimming habit of these fishes, especially those larger than 100 mm SL. An hypothesis is proposed that the swimbladder is of hydrostatic advantage to juvenile fishes which hover under jellyfish medusae and that it becomes nonfunctional in larger fishes which swim continuously. The scales are highly deciduous, and the skin is underlain by an extensive canal system, the function of which is unknown. The alimentary canal includes a small mouth with nipping teeth, a toothed, muscular pharyngeal sac which shreds food material, and numerous pyloric caeca and a long intestine which provide a great absorptive area.

Considerations of life history and ecology generally are of four species: *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus*. Spawn-

[1] This paper is based on a thesis presented to Harvard University in partial fulfillment of the requirements for the Ph.D. in Biology.

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ing occurs in the pelagic surface waters at varying distances from shore. The eggs and larvae are planktonic, the latter becoming capable of independent locomotion at a size of about 10 to 15 mm SL. The species occur in a wide range of salinities and variously inhabit all depths over the continental shelf and generally over a sand or mud bottom. The genus is essentially a tropical and warm temperate one with only two species, *P. triacanthus* and *P. simillimus*, reaching cooler waters. Seasonal movements appear to be most pronounced in *P. triacanthus*, the species occurring most abundantly in temperate regions. Fishes smaller than 100 mm SL associate with jellyfish medusae of several genera. This association is apparently important during the early critical growth phases of the fishes. *Peprilus* is a low-level carnivore; jellyfish medusae seem to be an important element in the diet, especially of juveniles. Other food items include a variety of small crustaceans, polychaete worms, and small fishes. Fishes of the genus are evidently significant forage fishes for a number of larger fishes, some of which are of great commercial importance. The economically important species of *Peprilus* are generally taken commercially in a region much smaller than the total range of the species, and this seems to reflect the pattern of migration and center of abundance of the particular species.

Disruption of the Tethys Sea in the Miocene apparently facilitated the segregation of the early members of the family Stromateidae and led to the evolution of the three extant and essentially allopatric stromateid genera. The formation of the Central American land bridge in the Pliocene, the emergence and submergence of land areas associated with the Pleistocene glacial and interglacial periods, and the prevailing current systems all appear to have been important in producing the current level of differentiation and speciation in the genus.

The elongate *P. snyderi* is considered to be the most primitive type, and the deep-bodied *P. paru* the most highly derived form in the genus. The Camin-Sokal method for deducing relationships of contemporaneous species is used to reconstruct a dendrogram of species relationships. Two somewhat subtle species groups are recognized in the genus, and each group is represented on both sides of the Central American isthmus. Character displacement is invoked as a possible mechanism to explain the existence of two apparently distinct populations of *P. triacanthus* in the Atlantic off the southeastern coast of the United States.

The distributions of the species of *Peprilus* appear to correspond generally to the major faunal provinces of the Atlantic Coast and the Pacific Coast of the Americas. The species generally traverse the zoogeographic subdivisions established from the study of small fishes inhabiting rocky shores. Sympatry involves the more diverse species, and the similar or closely related species tend to parallel one another in different oceans or displace one another latitudinally along a continuous coastline. Niche separation seems to be produced largely by spatial arrangement and ecological displacement.

INTRODUCTION

Purpose. One of the main purposes of this study has been to examine specimens of the stromateid genus *Peprilus* from throughout its geographic range, and to determine the limits of the species and the species relationships within the genus. The systematics of the species are considered in the first section of this paper and include a generic description, a key to the species, species descriptions and distributions, and an account of the geographic variation and ontogenetic change. The functional aspects of certain skeletal features, of body form, of the shape, position, and loss of fins, of the integument, and of the alimentary canal are considered in the second section.

Aspects of life history and ecology are considered in the third section and include a general account of the distribution in relation to certain physical factors, of seasonal distribution and abundance, of faunal associations, of larval and juvenile ecology, and of food habits. In this section, the discussion is concentrated on the better known and more accessible species. The final section concerns the evolutionary relationships and zoogeography of the genus and species. The proposed primitive and derived conditions in the genus are discussed, and the Camin-Sokal method is used to reconstruct a dendrogram of probable species relationships. The zoogeographical regions of the North and South American coasts are discussed in relation to the distribution of the species of *Peprilus*. A brief analysis is made of the degree of divergence in allopatric versus sympatric sets of species. The nature and level of speciation in the genus are considered and briefly compared to that of other types of coastal marine fishes.

Background. The fishes of the family Stromateidae comprise a small, well-defined marine group of some 12 to 15 species. Members of this perciform family occur on the continental shelf of oceans of both the Old and New Worlds; none have reached Australia or New Zealand. Haedrich (1967) recognized three genera in the family, *Stromateus*, *Pampus*, and *Peprilus*. These genera are allopatric except for a small area of overlap between *Stromateus* and *Peprilus* on the east coast of South America, and possibly a similar area on the west coast. *Stromateus* occurs along both coasts of South America, along the West African coast, and in the Mediterranean Sea; *Pampus* occurs from the Iranian Gulf to Japan; and, *Peprilus* is a New World genus of the east and west coasts of North, Central, and northern South America.

Stromateids are small (shorter than 18 inches), essentially pelagic, schooling fishes of coastal regions. Several of the species are commercially important. All possess

Figure 1. Pelvic bones of the three stromoteid genera: A = *Stromateus*; B = *Pampus*; C = *Peprilus*.

toothed pharyngeal sacs, a characteristic of the entire suborder Stromateoidei. According to Haedrich (1967), the Stromateidae are the apex in stromateoid evolution.

The genus *Peprilus* is the most speciose of the family, seven species being recognized in the current study. *Peprilus* is distinguished from the other stromateid genera by the combination of: deep body; large eye; long pectoral fin; two to four small spines ahead of the dorsal and anal fins; a ventral spine on the pelvic bone (Fig. 1); and, no pelvic fins. Differences also exist among the three genera in meristic values; in the number of epural elements in the caudal skeleton (three in one species of *Stromateus*, and two in all other species); and, in the number of branchiostegal rays (five in *Pampus*, six in the other two genera). At least three species of *Peprilus* form important fisheries. The flesh is considered to be of rich and delicate flavor.

Although the stromateid fishes are familiar coastal fishes often collected in large numbers, work on the group has been sporadic; and the relationships within the family have remained enigmatic. Much remains to be known of the life history and distribution of even the most common species. Early revisions of the family include those of Fordice (1884), Jordan and Evermann (1896; 1898), and Regan

(1902). Each of these studies, however, had only limited material available from restricted geographic areas. Haedrich (1967) has provided the most comprehensive and recent revision of the suborder; in his revision he arrived at a classification consisting of five families and fourteen genera. Caldwell (1961) has discussed the populations of one species, *Peprilus triacanthus*.

Studies of the early life history of the Stromateidae, particularly of *Peprilus*, have been largely confined to *P. triacanthus* and, to a lesser extent, *P. paru*. Such works include those of Kuntz and Radcliffe (1918), Hildebrand and Schroeder (1927), Pearson (1941), and Colton and Honey (1963).

Bigelow and Schroeder (1953) reviewed the life history and bionomics of *Peprilus triacanthus* (the butterfish) in the Gulf of Maine. T. J. Hart (1946) discussed at length the bionomics and seasonal distribution of *Stromateus maculatus* (= *S. brasiliensis*) off the Atlantic Coast of South America, and he compared these aspects of the species with those of *Peprilus triacanthus* off the Atlantic Coast of North America. Rege (1958), and Rege and Bal (1964), among others, have contributed to the knowledge of the life history of the species of *Pampus* off the coast of India.

A well-known aspect of the biology of stromateid fishes is their association with coelenterates, either medusae or siphonophores, in the pelagic environment. Mansueti (1963) has reviewed the literature on this association and has provided additional information on the interaction between *Peprilus paru* and the scyphomedusa, *Chrysaora quinquecirrha*. Stromateoids are also known to hover beneath flotsam and *Sargassum* weed (Besednov, 1960; Gooding and Magnuson, 1967). The hovering of stromateids beneath floating objects has not been well documented but probably does occur.

Kennedy and Milkman (1956) demonstrated that the lens of the butterfish, *Peprilus triacanthus*, transmits a considerable band of ultraviolet (UV) light. They indicated that a plankton-feeding fish, for example, might use UV sensitivity to locate areas of suspended matter, including organisms, by responding to the light of shortwave length scattered from such particles. Such a mechanism may facilitate the search for food or the location of jellyfish medusae.

Morphological and anatomical studies of stromateoid fishes are few. Haedrich's (1967) comparative study of the osteology of the group, and Bühler's (1930) extensive account of the digestive tract of the Centrolophidae and Stromateidae, are among the most notable contributions in this area. Gilchrist (1922) examined the teeth of the pharyngeal sac of stromateoids of South Africa, and Barnard (1948) revised and extended the former's work. Isokawa *et al.* (1965) have made additional contributions to the study of pharyngeal sacs and teeth.

Fossil stromateoids are few. Two new fossil genera have been found by Bonde (1966) in the lower Eocene of Denmark. However, no discoveries to date can be reliably referred to the Stromateidae.

Since the three stromateid genera are essentially allopatric, it is reasonable to treat each genus separately. This study is primarily concerned with the genus *Peprilus*, although reference to, and comparison with, other stromateids and other members of the suborder are made.

Three species of *Peprilus*, *P. paru*, *P. triacanthus*, and *P. simillimus*, are familiar fishes of North American coasts, but other members of the genus are less well known. Currently in fishery and faunal works, three genera are frequently recognized within what is here considered the genus *Peprilus*. The characters used for generic separation seem more reasonably to be criteria for delineating species; the species form a reasonably compact group. There are close species pairs in the genus, and there has been doubt as to whether certain populations constitute valid species. Active

speciation is in the process and creates uncertainty as to rank.

MATERIALS AND METHODS

The list of specimens examined for each species is included in the systematic section under the particular species in alphabetical order of museum and institutional names. Museum and institutional names are abbreviated as follows:

ANSP — Academy of Natural Sciences of Philadelphia
BM — Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
BC — University of British Columbia, Vancouver
CAS — California Academy of Sciences, San Francisco
FMNH — Field Museum of Natural History, Chicago
FSBC — Florida Board of Conservation Marine Laboratory, St. Petersburg
IMS — University of Texas Marine Science Institute at Port Aransas
LACM — Los Angeles County Museum
MCZ — Museum of Comparative Zoology, Harvard University
SIO — Scripps Institution of Oceanography, La Jolla
SU — Division of Systematic Biology, Stanford University
TABL — U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami
TU — Tulane University, New Orleans
USNM — United States National Museum, Washington, D.C.
UCLA — University of California, Los Angeles
UMML — Institute of Marine Sciences, University of Miami
UW — University of Washington, Seattle
WHOI[1] — Woods Hole Oceanographic Institution

Distributional and ecological data were obtained from three Bureau of Commercial Fisheries laboratories: Biological Laboratory, Woods Hole, Massachusetts; Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi; and, Fishery-Oceanography Center, La Jolla, California. Certain data on larval fishes were obtained from the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia.

Two lots of specimens collected on Cruise 16 of the R/V ANTON BRUUN were received from the Smithsonian Oceanographic Sorting Center, Washington, and are listed as uncatalogued specimens of *Peprilus medius* in the MCZ.

Three lots of specimens, two of *Peprilus burti* and one of *P. paru*, were collected personally at Port Aransas, Texas, and are listed as uncatalogued specimens in the MCZ.

Measurements were made point-to-point to the nearest tenth millimeter with a pair of fine point dial calipers. A dissecting microscope was used in measuring very small specimens.

Measurements made were: total length (TL); standard length (SL); head length; snout length; eye diameter; length of upper jaw; interorbital width; length of pectoral fin; predorsal distance I; predorsal distance II; preanal distance; maximum depth of body; and, least depth of caudal peduncle.

Counts in all but the largest specimens were made using a fine needle and under low magnification. Median fin-ray counts of very small specimens were made using transmitted, polarized light.

Counts made were: total dorsal fin elements (D); total anal fin elements (A); total pectoral fin elements (P); total gill rakers; precaudal and caudal vertebrae; and, lateral line scales.

Except for predorsal distances I and II, all measurements and counts conform to the methods of Haedrich (1967). Predorsal distance I is the distance from the tip of the snout to the base of the first element of the dorsal fin. Predorsal distance II is the distance from the tip of the snout to the anterior edge of the first free interneural.

Skeletal features were studied from radiographs and cleared-and-stained specimens. Radiographs suitable for counting vertebrae and for general osteological examination were made with three differ-

[1] These specimens will ultimately be deposited in the MCZ.

Table 1. Number* of Dorsal Fin-rays in Species of *Peprilus*.

Species	38	39	40	41	42	43	44	45	46	47	48	49	50	51
medius					1	1	7	33	40	34	33	7		2
ovatus			11	10	33	52	22	12	5					
simillimus				1	7	13	15	31	15	13	3			
snyderi						1		4	7	6	4	2		
burti	1	2	2	5	14	55	30	31	12	2	1			
triacanthus			4	5	7	25	30	53	15	7	4			
paru	1	2	8	23	29	59	23	25	5	3				

* Excluding spines.

ent types of industrial X-ray film at settings of 30 kilovolts and 200 milliampere-seconds or of 50–54 kilovolts and 100–150 milliampere-seconds, depending upon the type of film and size of specimens. The enzyme method of clearing-and-staining small vertebrates developed by W. R. Taylor (1967) was used exclusively in this study. Specimens ranging in size from six to 115 mm SL were successfully prepared using this method.

Drawings of each species were made from actual specimens with the aid of radiographs. Other drawings were made similarly, but with the aid of a camera lucida attached to a Wild dissecting microscope. The drawing of the digestive tract is semi-diagrammatic although made from a specific preparation.

Size-on-size and ratio-on-size diagrams are used for each species to show changes with growth and to make species comparisons.

Five characters, head length, eye diameter, body depth, length of pectoral fin, and depth of caudal peduncle, each expressed as a percentage of standard length, were plotted on standard length. The resulting scatter diagrams show trends and indicate change in size of body parts relative to standard length, but because of the wide scatter and curvilinearity, straight lines were not fitted to the data. Parr (1956) has advocated the use of ratio-on-size diagrams in preference to size-on-size diagrams. Ratios, however, have a greater inherent error than the measurements of which they are composed and are to be used cautiously (Simpson, Roe, and Lewontin, 1960: 18; Sokal, 1965: 346).

Five characters, eye diameter, length of upper jaw, length of pectoral fin, body depth, and depth of caudal peduncle, each expressed as a direct value, were plotted on standard length. Straight lines ($Y = A + BX$) were fitted to these size-on-size diagrams without transformation of the values by the method described by Bartlett (1949) and outlined by Simpson *et al.* (1960: 232). The regression lines for each character are presented in a single diagram for all the species, and the statistics of the lines are tabulated.

Measurements of either 24, 90, or 100 specimens were used for the size-on-size diagrams and of either 24, 90, or 109 specimens for the ratio-on-size diagrams. The specimens were randomly chosen from the broadest size and geographical ranges possible. Except for the few additional specimens used in certain of the ratio-on-size plots, measurements of the same specimens were used for both types of diagrams.

Computation of statistics describing the size-on-size regressions was performed at the Harvard Computation Laboratory on an IBM 7094 digital computer.

Unless indicated otherwise, other statistical procedures follow methods described by Simpson *et al.* (1960).

SYSTEMATICS

Genus *Peprilus* Cuvier, 1829

Rhombus Lacépède, 1800: 60. (Type species: *Chaetodon alepidotus* Linnaeus, 1766: 460, by monotypy. Charleston, South Carolina. Pre-

Table 2. Number* of Anal Fin-rays in Species of *Peprilus*.

Species	35	36	37	38	39	40	41	42	43	44	45	46	47
medius						1	2	17	44	41	32	16	4
ovatus						7	14	29	50	20	20	6	
simillimus	1		6	15	30	28	12	5	2	1			
snyderi						3	8	1	7	4			
burti	1	1	4	15	51	43	26	11	3				
triacanthus			2	10	33	40	34	23	9	1			
paru	1	2	7	20	32	29	31	30	18	4	2		

* Excluding spines.

occupied by *Rhombus* Humphrey, 1797, Mollusca.)

Peprilus Cuvier, 1829: 213. (Type species: *Sternoptyx gardenii* Bloch and Schneider, 1801: 494; by subsequent designation of Gill, 1862: 126. Charleston, South Carolina. A synonym of *Chaetodon alepidotus* Linnaeus, 1766: 460.)

Poronotus Gill, 1861: 35. (Type species: *Stromateus triacanthus* Peck, 1804: 48, fig. 2, pl. II, by monotypy. Piscataqua River, New Hampshire.)

Palometa Jordan and Evermann, 1896: 966. (Subgenus. Type species: *Stromateus palometa* Jordan and Bollman, 1889: 156, by original designation. Elevated to generic rank, Jordan and Evermann, 1898: 2849. Panama Bay, Pacific Ocean.)

Simobrama Fowler, 1944: 2, fig. 2. (Type species: *Seserinus xanthurus* Quoy and Gaimard, 1824: 384, by original designation. Rio de Janeiro, Brazil. A synonym of *Stromateus paru* Linnaeus, 1758: 248.)

Diagnosis. The genus *Peprilus* is distinguished from other stromateid genera by the combination of deep body, large eye, long pectoral fin, two to four bladelike spines anterior to the rays of the dorsal and anal fins, a ventral spine on the pelvic bone, and no pelvic fins. Also, *Peprilus* is distinguished specifically from the stromateid genus *Pampus* in having six rather than five branchiostegal rays and in having a movable rather than a fixed maxillary bone. *Peprilus* is further distinguished from *Stromateus* in having 29 to 36 vertebrae rather than approximately 42 to 48.

Description. Body deep, ovate to elongate, depth 35 to 87 per cent of standard length, highly compressed. Caudal peduncle short, slender, and compressed. Dorsal and ventral profiles convex and similar; anterior dorsal profile slightly to strongly convex. Snout short and blunt; jaws equal; maxilla just reaching to line of anterior margin of eye; eye large with surrounding adipose tissue reaching to nostrils; eye diameter either as great or greater than length of snout. Nostrils double, anterior round, posterior a slit, directly anterior to eye, near end of snout. Dorsal and anal fins with long base, similar to each other, either slightly, moderately, or extremely falcate, as produced by elongation of the first 10 to 13 rays; dorsal and anal coterminal just anterior to caudal peduncle. Dorsal fin with two to four small, bladelike spines anterior to and continuous with 40 to 51 fin-rays; spines often irregular in shape, free surface jagged or crenulated, anterior spine pointed on both ends; third or fourth spine often difficult to distinguish from anteriormost rays. Anal fin equal to or shorter than dorsal, with two or three (rarely four) small spines preceding and continuous with the 35 to 47 fin-rays; spines usually easier to distinguish than in dorsal since rays of anal are more distinctly segmented. Pectoral fin lateral,

Table 3. Number of Pectoral Fin-rays in Species of *Peprilus*.

Species	17	18	19	20	21	22	23	24
medius				2	10	52	75	19
ovatus			1	9	74	54	12	
simillimus			1	15	65	25	1	
snyderi					3	10	9	
burti			2	16	60	65	5	
triacanthus	1	1	4	51	71	21		
paru		1	1	17	39	63	40	11

Table 4. Total Number of Gill Rakers in Species of *Peprilus*.

Species	20	21	22	23	24	25	26	27
medius				15	47	67	24	1
ovatus		2	7	56	63	17	1	
simillimus				19	29	19	8	
snyderi				6	6	4	2	
burti		1	14	26	26	3	1	
triacanthus			4	8	10	11		
paru	9	39	44	6				

just below level of eye, long, winglike, lower rays much shorter than upper ones, base of fin slightly inclined, becoming relatively longer with age, often short and fanlike in larvae and small juveniles; 17 to 24 rays. No pelvic fins, a small spine on the posterior end of the fused pelvic bones projects posteroventrally through the skin at mid-ventral line below base of pectoral fin; pelvic bones closely adjacent anteriorly, fused posteriorly. Edge of coracoid may project underneath head at level of preopercular margin. Caudal fin long to very long, deeply forked, about 18 to 40 per cent of total length; lobes equal. Scales small, cycloid, irregular in shape, deciduous; occasionally with small, blunt, knoblike structures on posterior surface; scales often crowded, usually absent in preserved material; cheek, suborbital area, preopercle, and sometimes opercle scaled; top of head and nape generally scaleless; scales extending onto caudal, dorsal, and anal fins, less so on pectorals, usually only to base of latter. Lateral line of trunk of simple, tubed scales which are often less deciduous than those of rest of body; lateral line above intermuscular septum, either following dorsal profile or more highly arched anteriorly, extending from cleithrum onto caudal peduncle to base of caudal fin. A branch of lateral line extends from immediately above eye posteriorly to head of hyomandibula where it joins a similar branch then turns upward toward middorsal line in a wide, bony tract; cephalic lateral line of pores and branching canals on cheek, opercular area, snout, lower jaw, and top of head. Subdermal canal system on body, top of head and nape; main canal along intermuscular septum with numerous, parallel side-branches; often only partially visible or completely invisible in preserved material. Skin of top of head underlain by a series of small, dendritic canals extending backward over nape. In two species there is an irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. A third species often has a series of slightly smaller, irregularly-spaced pores along entire dorsal surface. All species have very small pores scattered over body, apparently in association with the subdermal canal system. Head about 25 to 40 per cent of standard length, depending upon species and age. Premaxilla not protractile; maxilla movable. Lacrimal bone small, end of maxilla exposed when mouth closed. No supramaxilla. Jaw teeth small, uniserial, close-set; premaxillary teeth slightly recurved, either pointed and simple, or, in two species, with three small cusps; in at least

Table 5. Number of Vertebrae in Species of *Peprilus*.

	Precaudal				Caudal						
Species	12	13	14	15	16	17	18	19	20	21	22
medius		173	8						20	153	8
ovatus	3	154					5	143	9		
simillimus		158	2			138	22				
snyderi			3	20						20	3
burti		273			5	262	6				
triacanthus		279				7	62	208	2		
paru	1	181			3	176	3				

two other species both types of premaxillary teeth may be present; teeth of lower jaw with three to five small cusps; slightly more closely spaced than premaxillary teeth. Vomer, palatines, and basibranchials toothless. Gill membranes united across isthmus, divided from about level of anterior part of eye. Opercle and preopercle thin, flat; preopercle finely striated; opercular margins entirely with two flat, blunt, ill-defined spines. Gill rakers similar in all species, slightly more than one-half the length of filaments; with fine teeth on inner edge; closely set; six to nine on epibranchial, one at junction of elements, and 13 to 18 on lower elements of first arch (cerato- and hypobranchials). Pseudobranch small. Six branchiostegal rays, four on ceratohyal, two on epihyal. Vertebrae, 12 to 15 precaudal, 16 to 22 caudal, 29 to 36 total. Three free interneural bones anterior to dorsal fin. Sclerotic bones well ossified. Toothed pharyngeal sac behind last gillarch as in all other stromateoid fishes, joining tubular esophagus; stomach a simple sac; intestine long and in loops, about two and one-half to three times the standard length of the body; pyloric caeca numerous, short, in a dendritic mass adjacent to stomach. Swimbladder thin-walled, physoclistous, continuous with dorsal peritoneum; easily deflated; possibly nonfunctional or absent in adults; found only in fish smaller than 80 to 100 mm SL; not yet seen in all species. Buccal and pharyngeal cavities light in color; peritoneum silvery, with peppering of black pigment that is more dense dorsally. Gonads paired, in posteroventral region of body cavity; ovary in mature and maturing specimens elongate, yellow, and granular; eggs in ripe ovary spherical, yellowish, less than 1 mm in diameter; testis in mature and maturing individuals elongate, thin, yellowish white, and smooth in texture. No external sexual dimorphism apparent.

Color in life iridescent bluish or greenish silver dorsally to silver ventrally. At least one species often has large, dark spots on the dorsal and upper ventral surface. Color in preservative varying from bluish brown to brown dorsally to silver ventrally or body completely brown or bluish brown. Individual melanophores conspicuous in specimens up to about 80 to 100 mm SL, dense and small dorsally, larger and more dispersed ventrally. Anal and dorsal fins with distinct melanophores on membranes between fin-rays, slightly less evident on the paler caudal and pectoral fins. Eye usually darker than rest of body, lens opaque surrounded by iris which is either completely black or partly black and partly yellowish white.

Key to the Species of *Peprilus*

Ranges of proportional measurements in thousandths of standard length and ranges of meristic values are each followed by the mean or two different means (when for two species) in parentheses.

1a. Row of about 17 to 25 relatively large pores immediately below anterior half of dorsal fin; premaxillary teeth usually with three small cusps 2

1b. No row of pores below anterior half of dorsal fin; premaxillary teeth pointed, simple 3

2a. Body elongate, shallow to moderately deep 364 to 600 ($\bar{x}$ 458); eye moderately large, 061 to 133 (086); caudal vertebrae 17 to 20, usually 19, rarely 17 or 20; dorsal and upper ventral surface in adults often mottled with dark spots ..... *P. triacanthus* (Peck, 1804) p. 197, Figs. 21, 22.

2b. Body moderately elongate, moderately deep to deep, 460 to 640 ($\bar{x}$ 551); eye large, 065 to 144 (100); caudal vertebrae 16 to 18, usually 17; dorsal or upper ventral surface rarely if ever mottled ..... *P. burti* Fowler, 1944 p. 192, Fig. 19.

3a. Dorsal and anal fins except in larvae and juveniles smaller than 50 to 75 mm SL moderately to extremely falcate, the longest anal ray six or more times the length of the shortest anal ray; dorsal often slightly less falcate 4

3b. Dorsal and anal fins only slightly falcate, the longest dorsal and anal rays less than six times the length of the shortest of each 5

4a. Body ovate, very deep, 565 to 877 ($\bar{x}$ 710); dorsal rays 38 to 47, usually 41 to 45 (42.9); gill rakers 20 to 23, usually 21 or 22 (21.5); caudal vertebrae 16 to 18, usually 17 .....

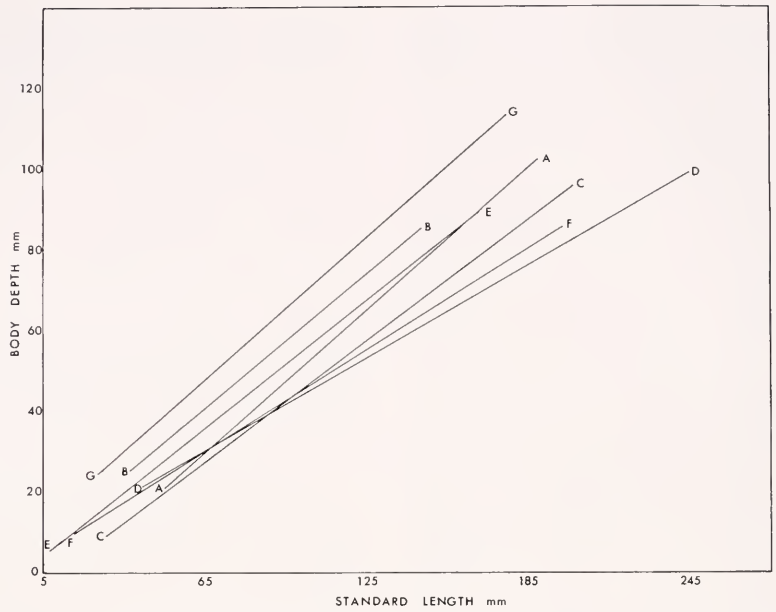


Figure 2. Regression of body depth on standard length for each species of *Peprilus*: A = *P. medius*; B = *P. ovatus*; C = *P. simillimus*; D = *P. snyderi*; E = *P. burti*; F = *P. triacanthus*; G = *P. paru*. Statistics in Table 6.

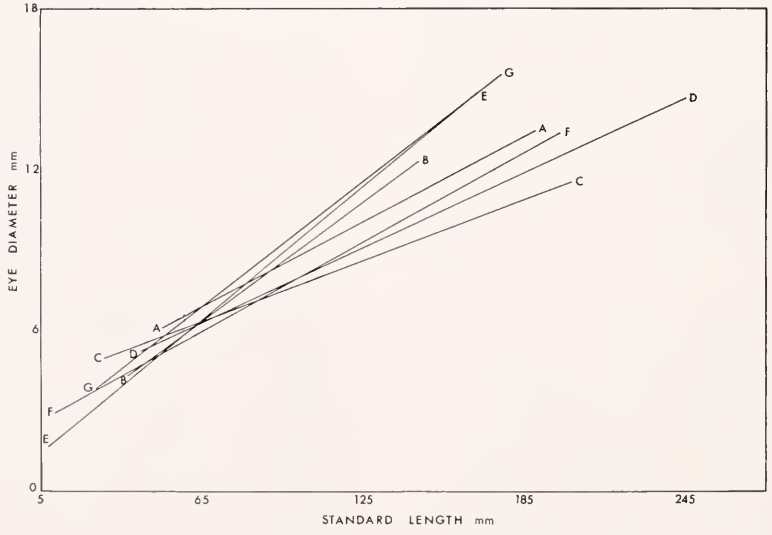


Figure 3. Regression of eye diameter on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

— *P. paru* (Linnaeus, 1758) p. 202, Fig. 24.

4b. Body moderately elongate, moderately deep to deep, 459 to 618 ($\bar{x}$ 529); dorsal rays 42 to 51, usually 45 to 48 (46.7); gill rakers 23 to 27, usually 24 to 26 (24.7); caudal vertebrae 20 to 22, usually 21 ——— *P. medius* (Peters, 1869) p. 175, Fig. 8.

5a. Body ovate, deep, 542 to 676 ($\bar{x}$ 619); eye moderately large, 078 to 115 (093); snout length considerably less than eye diameter, 052 to 074 (063); dorsal spines 3 or 4, most frequently 4; often a series of irregularly-spaced, medium-sized pores visible along dorsal surface; total vertebrae 31 to 33, usually 32 (32.0) ——— *P. ovatus* sp. n., p. 182, Fig. 10.

5b. Body elongate, shallow to moderately deep, 371 to 517 ($\bar{x}$ 427, 461); eye small, 050 to 119 (070, 073); snout length about equal to eye diameter, 058 to 083 (068, 070); dorsal spines 2 to 4, usually 3; no series of medium-sized pores usually visible along dorsal surface; total vertebrae 30, 31, or 36 ——— 6

6a. Dorsal rays 43 to 49, usually 45 to 48 ($\bar{x}$ 46.5); anal rays 40 to 44 (42.0); caudal vertebrae 21 or 22, usually 21; total vertebrae 36 ——— *P. snyderi* Gilbert and Starks, 1904 p. 189, Fig. 16.

6b. Dorsal rays 41 to 48, usually 43 to 47 ($\bar{x}$ 44.8); anal rays 35 to 44, usually 38 to 41 (39.5); caudal vertebrae 17 or 18, usually 17; total vertebrae 30 or 31 ——— *P. simillimus* (Ayres, 1860) p. 185, Fig. 13.

Peprilus medius (Peters, 1869)

Figures 8, 18a

Stromateus medius Peters, 1869: 707 (original description, Mazatlán, México, holotype seen, 138.4 mm SL, BM 7073); Jordan, 1883: 284; Fordice, 1884: 314.

Stromateus palometa Jordan and Bollman, 1889: 156 (original description, Pacific Ocean, off coast of Panama, 8°16′30″N, 79°37′45″W, ALBATROSS 2804, holotype not seen; four paratypes seen, 50.0 to 58.3 mm SL, SU 434).

Rhombus (*Palometa*) *palometa,* Jordan and Evermann, 1896: 966, *Palometa* erected as subgenus.

Rhombus (*Palometa*) *medius,* Jordan and Evermann, 1896: 967.

Palometa palometa, Jordan and Evermann, 1898: 2849, subgenus *Palometa* elevated to generic level; Jordan, Evermann, and Clark, 1930: 267.

Palometa media, Jordan and Evermann, 1898: 2849; Jordan, Evermann, and Clark, 1930: 267.

Peprilus palometa, Gilbert and Starks, 1904: 85; Meek and S. F. Hildebrand, 1925: 412; Haedrich, 1967: 107.

Peprilus medius, Gilbert and Starks, 1904: 88; Meek and S. F. Hildebrand, 1925: 413; Haedrich, 1967: 107.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BM 7073 (1:138.4 mm, holotype of *Stromateus medius* Peters, Mazatlán, Mexico); BC 56–164 (1:113.0, Paita, Peru, CS); *BC 56–233 (5:143.7–186.0, Paita, Peru); *BC 59–668 (28:108.6–144.0, Pacific Ocean, Panama Bay near Panama City); *BC 59–685 (6:119.3–139.5, Pacific Ocean, Chiman area SE of Panama City); *BC 59–686 (3:125.7–139.6, Pacific Ocean, near Puerto Obaldia, Panama); *BC 59–687 (4:124.8–174.0, Panama City market); *BC 60–25 (1:143.5, Mexico, Golfo de Tehuantepec, Puerto Arista to Salina Cruz); *BC 60–115 (2: 37.4, 144.5, Pacific Ocean, Taboga I., off Panama); BC 61–126 (1:189.0, Mex., Acapulca market); *BC 61–151 (1:131.0, Mazatlán, Mex.); *FMNH 20500 to 20503 (4:123.5–158.5, Panama City market, February-March, 1911); *FMNH 73840 (8: 109.6–185.0, Mex., 1–5 miles off Chiapas coast at Guatemala border to above San Benito, 18–27 m, 14–18 December 1954, 5 radiographed); *LACM 6545–2 (1:112.9, Sinaloa, Mex., 30 August 1962); *LACM 6917–8 (1:163.2, Pacific Ocean, El Savador, Fondo del Mar, August, 1965); *MCZ uncat. (15:111.2–140.6, R/V ANTON BRUUN Cr. 16, Sta. 624E, 04°53′S, 81°23′ W, 75–91 m, 2 June 1966, 14 radiographed); *MCZ uncat. (11:75.3–90.8, R/V ANTON BRUUN Cr. 16, Sta. 624b, 04°48′S, 81°17′W, 16 m, 2 June 1966, 1 CS); *SIO H51–324 (1:141.3, Golfo de Fonseca, Honduras, about 13°00′N, 87°40′ W, 1 August 1951, M/V RENOWN); *SIO 55–58 (1:130.5, Pacific Ocean, between San Diego, California, and Ecuador, dipnet from tuna clipper, July, 1955); *SIO 59–263 (5:76.5–80.5, Sinaloa, Mex., off Rio San

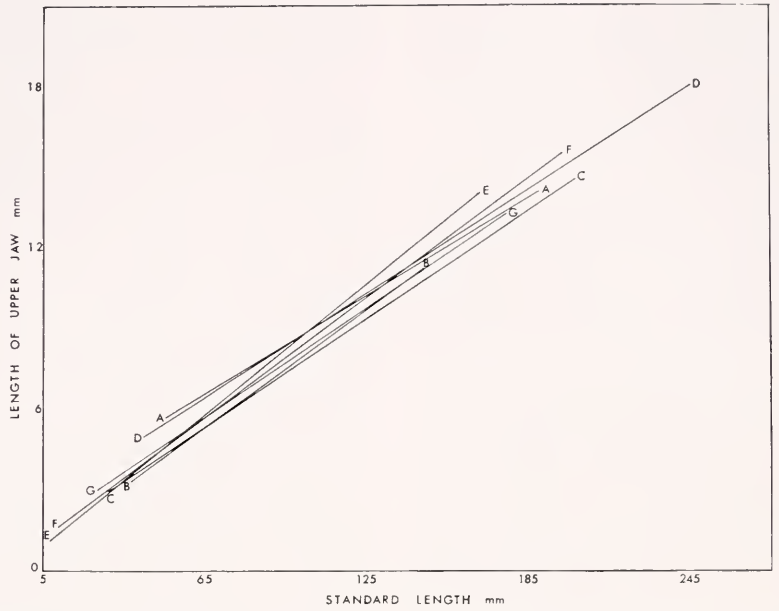


Figure 4. Regression of length of upper jaw on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

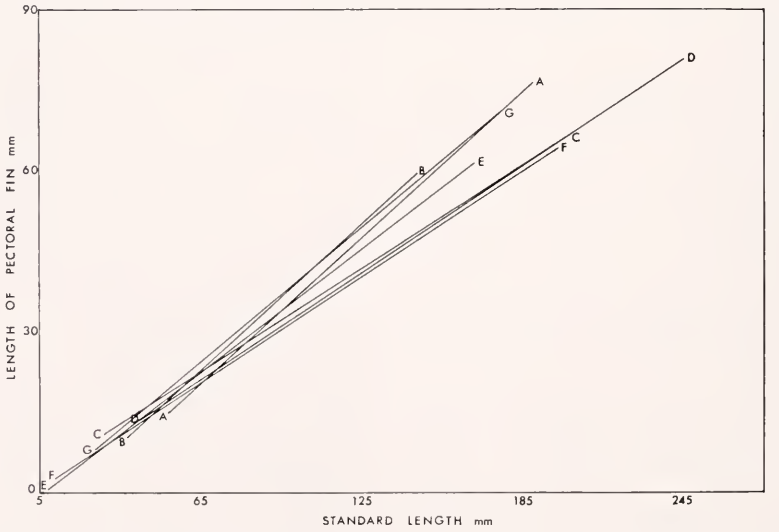


Figure 5. Regression of length of pectoral fin on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

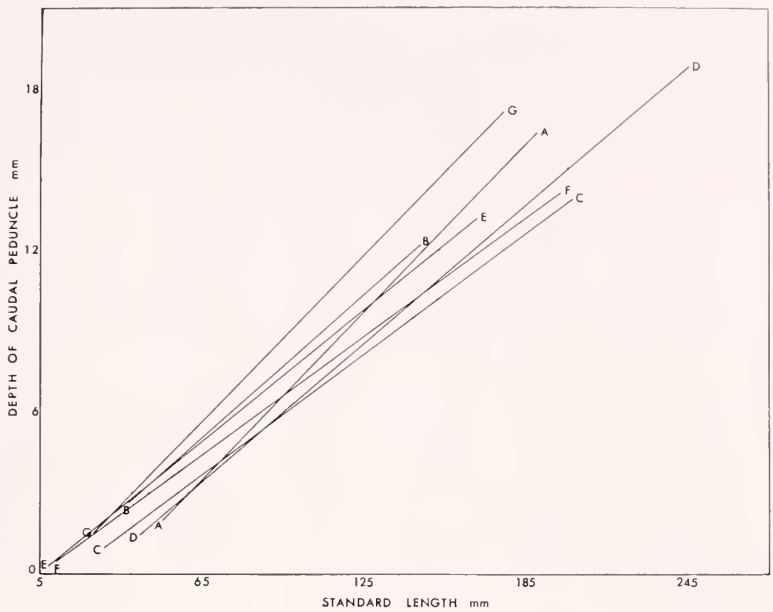


Figure 6. Regression of depth of coudal peduncle on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

Lorenzo, 23°50.5′N, 107°18.2′W, 77–88 m, 16 May 1959, SIO Vermilion Sea Expedition, 4 radiographed; *SIO 64–749 (1:112.4, Panama, off San Carlos, 17 August 1961); *SU 434 (4:50.0–58.3, paratypes of *Stromateus palometa* Jordan and Bollman, 1889, off coast of Panama, "N, 79°8°16′3037′45″W, ALBATROSS Sta. 2804, 86 m); *SU 1867 (1:68.0, same as SU 434 above, part of type material of *Stromateus palometa*, incorrectly labeled as From Galapagos Is., according to S. F. Hildebrand (MS)); *SU 6998 (5:136.0–180.4, Panama); *USNM 41272 (1:65.0, Pacific Ocean, ALBATROSS Sta. ?); *USNM 200351 (1:150.0, Peru, Caleta Cruz, Tumbes, 37–55 m, 25 March 1965); *UCLA W51–246 (2:140.0, 146.5, Ecuador, vicinity of Guayaquil, 16 November 1951); *UCLA W53–275 (19:110.6–178.0, Panama Bay between Panama city and Punta Gorda, 4–27 m, 1–5 July 1953); UCLA W53–311 (2: 109.7, 111.8, Panama, between Islas Perlas and Isla Otogne, 8°32′10″N, 79°21′11″W, 64 m, 19 March 1953); *UCLA W54–55 (1:121.3, Costa Rica, S of Golfo de Nicoya, 9–27 m, 29 November 1952); *UCLA W54–167 (1:141.2, Costa Rica, Golfo de Nicoya, 5–8 m, 16–18 April 1952); *UCLA W54–334 (6:121.8–163.5, Panama Bay, mouth of Anton River, 15 m, 21 May 1954); *UCLA W56–112 (2:111.1, 112.5, Gulf of California, Sinaloa, Mex., Bahía Topolobampo, from mouth to 6–9 miles N, 2–9 m, 22 May 1956); *UCLA W56–113 (15:84.5–115.4, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, 6–11 m, 24 May 1956); *UCLA W56–115 (1:96.0, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, in main channel from islands E of town to Punta Copas, 13 m, 31 May 1956); *UCLA W56–117 (11:84.7–108.2, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, N of entrance, 9–13 m, June, 1956); *UCLA W56–123 (2:109.6, 112.2, Gulf of Calif., Sinaloa, Mex., vicinity of I. de Altamura, 25°15′N, 108°30′W, 9 m, 10 March 1956); *UCLA W58–46 (1:163.8, Gulf of Calif.,

TABLE 6. STATISTICS DESCRIBING REGRESSIONS ($y = a + bx$) OF BODY MEASUREMENTS ON STANDARD LENGTH, FIGS. 2–6, FOR THE SPECIES OF *PEPRILUS*. $\bar{x}$ = mean size (SL); $\bar{y}$ = mean of body proportion; N = number of specimens; a = y intercept; b = slope; CL-b = 95% confidence limits for b; r = correlation coefficient.

BODY PROPORTION	$\bar{x}$	$\bar{y}$	N	a	b	CL-b	r
Body Depth							
medius	121.6	63.1	100	−8.4	0.59	0.49–0.69	0.96
ovatus	85.6	52.1	90	4.6	0.56	0.50–0.62	0.99
simillimus	123.8	57.3	100	−4.6	0.50	0.43–0.57	0.97
snyderi	170.0	70.8	24	5.4	0.38	0.30–0.46	0.99
burti	82.0	44.9	90	1.7	0.53	0.46–0.60	0.99
triacanthus	108.4	48.3	100	3.1	0.42	0.35–0.49	0.98
paru	91.6	63.5	100	9.7	0.58	0.48–0.68	0.95
Eye Diameter							
medius	121.6	9.9	100	3.5	0.052	0.042–0.062	0.93
ovatus	85.6	7.9	90	1.5	0.074	0.067–0.081	0.97
simillimus	123.8	8.6	100	3.9	0.038	0.027–0.049	0.81
snyderi	170.0	11.2	24	3.3	0.046	0.037–0.055	0.97
burti	82.0	7.8	90	1.0	0.083	0.073–0.093	0.90
triacanthus	108.4	8.4	100	2.4	0.056	0.046–0.066	0.84
paru	91.6	9.0	100	1.8	0.078	0.070–0.086	0.90
Length of Upper Jaw							
medius	121.6	10.0	100	2.60	0.061	0.054–0.068	0.96
ovatus	85.6	6.8	90	0.59	0.072	0.065–0.079	0.98
simillimus	123.8	9.3	100	1.00	0.067	0.060–0.074	0.96
snyderi	170.0	13.2	24	2.20	0.065	0.060–0.070	0.99
burti	82.0	7.1	90	0.43	0.081	0.077–0.085	0.99
triacanthus	108.4	8.9	100	0.81	0.075	0.069–0.081	0.98
paru	91.6	7.5	100	1.30	0.068	0.062–0.074	0.97
Length of Pectoral Fin							
medius	122.2	47.0	100	−6.10	0.43	0.39–0.47	0.97
ovatus	85.8	32.4	90	−6.60	0.45	0.40–0.50	0.97
simillimus	123.8	41.6	100	1.70	0.32	0.25–0.39	0.93
snyderi	170.0	57.4	24	−0.57	0.33	0.27–0.39	0.99
burti	81.5	28.4	90	−3.00	0.38	0.32–0.44	0.98
triacanthus	108.3	34.9	100	−1.20	0.33	0.26–0.40	0.97
paru	92.1	35.9	100	−2.50	0.42	0.38–0.46	0.99
Depth of Caudal Peduncle							
medius	121.6	9.4	100	−3.30	0.104	0.088–0.120	0.95
ovatus	85.6	6.9	90	−0.67	0.090	0.077–0.103	0.97
simillimus	123.8	8.1	100	−1.10	0.075	0.062–0.088	0.95
snyderi	170.0	12.4	24	−2.10	0.085	0.079–0.091	0.99
burti	82.0	6.3	90	−0.37	0.081	0.074–0.088	0.99
triacanthus	108.4	7.6	100	−0.31	0.073	0.064–0.082	0.97
paru	91.6	8.4	100	−1.04	0.103	0.095–0.111	0.97

Sinaloa, Mex., S of Bahía Topolobampo, off I. San Ignacio and I. Macapule, 7–13 m, 10–14 February 1958); UCLA W58-218 (1:126.2, Gulf of Panama, 10 miles WNW I. Pacheca, 08°44′N, 79°13′W, 48 m, 8 March 1957); *UCLA W58-303 (14:124.3–156.0, Panama Bay, Punta Bay, Punta Chame and Punta Anton, 6–27 m, 6–9 September 1958); *UCLA W58-304 (8: 100.4–131.6, Panama Bay, between Punta de Hicacal and Rio Pasiga, 3–4 m, 7–9 September 1958); UCLA W58-305 (1:

Figure 7. Distribution of the species of *Peprilus*.

136.0, Panama Bay between Rio Chico and Punta de la Plata, 3–6 m, 7–11 September 1958).

Diagnosis. *P. medius* is moderately elongate and is the only Pacific Coast species in the genus with moderately to extremely falcate dorsal and anal fins. Specifically and aside from the length of the lobes of the dorsal and anal fins, it is distinguished from the similar *P. ovatus* by having usually 21 rather than 19 caudal vertebrae; a more elongate body – mean body depth of 529 compared to 619 for *P. ovatus*, each in thousandths of SL; a mean number of dorsal fin-rays of 46.7 compared to 42.8 for *P. ovatus;* and usually three dorsal spines rather than frequently four as in *P. ovatus.* It is distinguished from *P. snyderi* by having a deeper body – mean body depth of 529 compared to 427 for *P. snyderi*, each in thousandths of SL; an eye diameter greater than the length of the snout; and 33 to 35 rather than 36 total vertebrae; and from *P. simillimus* by having a deeper body – mean body depth of 529 compared to 461 for *P. simillimus*, each in thousandths of SL; a mean number of anal fin-rays of 43.9 compared to 39.5 for *P. simillimus;* and 33 to 35 rather than 30 or 31 total vertebrae. The species differs from the related *P. paru* in the Atlantic by having a more elongate body – mean body depth of 529 compared to 710 for *P. paru*, each in thousandths of SL; a mean number of dorsal fin-rays of 46.9 compared to 42.9 for *P. paru;* and 33 to 35 rather than 29 to 31 total vertebrae.

Description. Proportional measurements are given in Table 7 and meristic values in Table 8. Body moderately elongate, moderately deep to deep, compressed; anterior dorsal profile moderately convex.

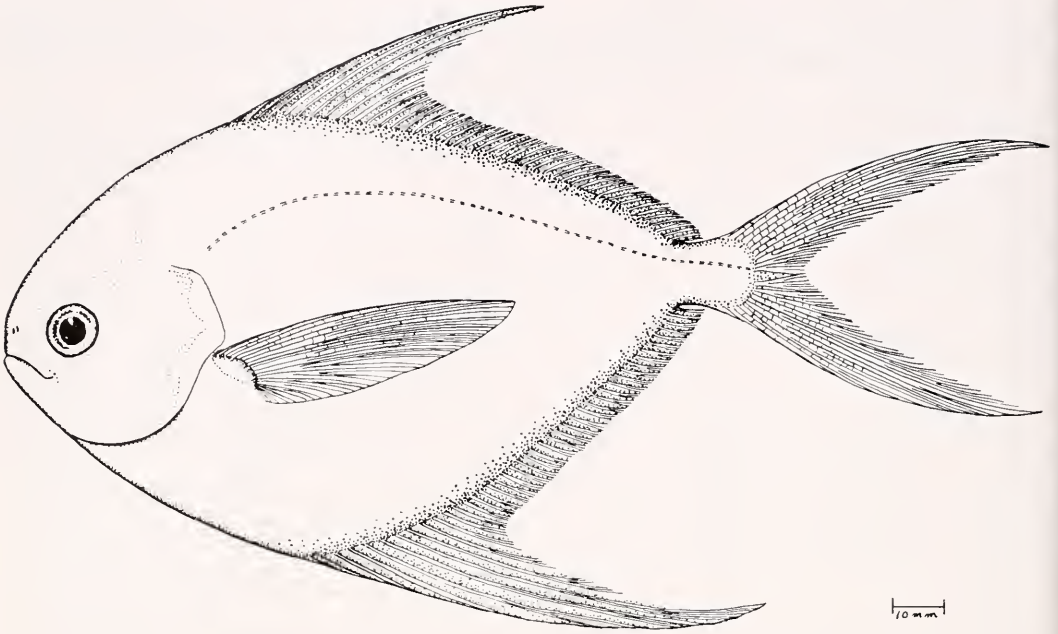


Figure 8 *Peprilus medius*, 141.3 mm SL, Golfo de Fonseca, Honduros, SIO H51-324.

Eye diameter greater than length of snout. Dorsal and anal fins moderately to extremely falcate, longest rays of anal six or more times the length of shortest anal ray; dorsal often slightly less falcate; both usually becoming more falcate with age. Dorsal and anal with three or four (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 22 to 40 per cent of total length. Subdermal canal system indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. Premaxillary teeth slightly recurved, pointed, simple. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 250 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from four to about 11 (Table 7) and from 1.2 to about 3.6 for meristic characters (Table 8). According to Simpson *et al.* (1960), V is a good measure of relative dispersion and usually a suitable measure of variability; it is useful in comparing the variability of samples or species.

The sample size of *P. medius* (Table 7) used is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all the species of *Peprilus,* is relatively constant (Table 5).

Geographic variation. No decided geographic variation was detected in *P. medius.* A slight tendency, however, for the median fins to be longer in the lower latitudes of the distribution was noted, but was too small to quantify.

Ontogenetic change. Few and moderate changes accompany growth in *P. medius* in a size range of about 50 to 189 mm SL.

Table 7. Proportional Measurements of *Peprilus medius*. N = number of specimens; R = range of values; $\bar{x}$ = mean; SE = standard error of mean; V = coefficient of variation. Size range, 50.0–189.0 mm SL; mean size, 124.4 mm SL.

	N	R	$\bar{x}$	SE	V
In thousands of SL:					
Head length	162	260–384	295	1.61	6.96
Snout length	162	046–080	060	0.37	7.95
Eye diameter	162	061–113	082	0.64	9.87
Length of upper jaw	162	069–111	082	0.62	9.59
Interorbital width	162	077–109	091	0.41	5.78
Length of pectoral fin	160	290–442	386	2.13	6.99
Predorsal distance I	162	351–436	390	1.27	4.14
Predorsal distance II	162	239–312	273	1.18	5.52
Preanal distance	162	369–496	434	1.50	4.39
Maximum depth of body	182	459–618	529	2.34	5.98
Least depth of caudal peduncle	162	058–094	078	0.68	11.04
In thousandths of HL:					
Snout length	162	152–284	203	1.32	8.31
Eye diameter	162	235–333	279	1.29	5.86
Length of upper jaw	162	225–333	278	1.10	5.01
Interorbital width	162	240–352	307	1.49	6.18

Table 8. Meristic Values of *Peprilus medius*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	158	42–51	46.7	0.12	3.19
Anal fin-rays*	157	40–47	43.9	0.11	3.03
Pectoral fin-rays	158	20–24	22.6	0.07	3.63
Total gill rakers	154	23–27	24.7	0.07	3.56
Total vertebrae	181	33–35	34.0	0.03	1.21
Lateral-line scales	23	105–117	–	–	–

* Excluding spines.

With growth, head length and eye diameter decreases in size relative to SL (Fig. 9). The correlation coefficient in the size-on-size regression of eye diameter is, however, relatively high (Fig. 3; Table 6). Body depth, length of the pectoral fin, and depth of the caudal peduncle increase in size relative to SL with growth up to about 125 to 150 mm SL, beyond which the values become nearly constant (Figs. 9 and 12). The anterior lobes of the dorsal and anal fins tend to increase in length with growth (compare Figs. 8 and 18a).

Distribution (Fig. 7). *P. medius* is known from off the Pacific Coast of northern South America, Central America, and Mexico northward to the southern region of the Gulf of California. The southern extent of the range is near Paita, Peru, about 5°S, and just south of Golfo de Guayaquil. The northern known limit of the range is near Bahía Topolobampo, Sinaloa, Mexico, about 25°30′N. One specimen is known from the Galapagos Islands, but was not examined in this study (128 mm SL, TABL uncat.).

Taxonomic comments. The holotype of *Stromateus medius* Peters is very similar to specimens identified as *Peprilus* or *Palometa palometa*. The supposed anal ray count of 32 for the holotype of *S. medius* is incorrect; the correct value is 42, within the range of values for *P. palometa*. The count can be made accurately only by examining the radiograph of the holotype since the anterior portion of the anal fin is externally mutilated. I have thus placed the two names, *S. medius* and *P. palometa*, in synonymy of *Peprilus medius*.

It has been a common practice to identify questionable stromateids from the Gulf of California with either *Palometa media* or *Peprilus medius*. A distinct population does exist in the northern Gulf of California and is described below as new.

Peprilus ovatus sp. n.

Figures 10, 18b

Holotype. A 128.7 mm SL specimen, USNM 203304; 3–5 February 1949, Gulf of California, Sonora, Mexico, about 20 miles SW of Golfo de Santa Clara near the mouth of the Colorado River, shrimp trawl, 13 to 27 m depth.

Paratypes. Two, 56.6, 118.4 mm SL, LACM 30175–1 and –2; data as above for holotype.

Two, 56.9, 123.9 mm SL, MCZ 46202; data as above for holotype.

Thirty-six, 38.3–126.0 mm SL, UCLA W49–55; data as above for holotype.

Additional material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). All specimens are from the northern Gulf of California. *CAS 24158 (15:41.4–127.5 mm, Sonora, Mexico, 10 miles off Santa Clara, 5 February 1952, 2 CS); *SIO H47–53 (2:62.5, 67.7, Baja California, between San Felipe and mouth of Colorado River, 31°18′–22′N, 114°47′–50′W, 4–9 m, 6–9 April 1947, shrimp trawler FELIPE ANGELES); *SIO 58–164 (3:51.5–75.6, Baja Calif., 10 miles N of San Felipe, 4 April 1956); *SIO 63–484 (6:55.9–84.3, mouth of Colorado R.); *UCLA W49–91 (36:37.5–124.8, Baja Calif., about 10 miles SE of San Felipe, February, 1950); *UCLA W49–422 (4:70.6–78.0, Baja Calif., between San Felipe and mouth of Colo. R., 6–9 April 1947); *UCLA W49–423 (2:80.8, 84.1, Baja Calif., San Felipe Bay, 10 April 1947); UCLA W49–429 (1:83.5, Baja Calif., off Punta Diggs S of San Felipe, 10 April 1947); *UCLA W53–196 (29:63.2–88.0, Baja Calif., between San Felipe and mouth of Colo. R., 6–9 April 1947, same collection as UCLA W49–422); *UCLA W53–198 (3:69.0–87.9, Baja Calif., San Felipe Bay, 10 April 1947); *UCLA W54–366 (1:145.2, Baja Calif., 2 to 3 miles N of Punta Diggs, about 7 miles S of San Felipe, 11 m, 23 September 1954, shrimp trawler SAN LUIS); *UCLA 55–2 (9:45.4–132.5, Baja Calif., Punta Diggs, 9 miles E of San Felipe, 24 m, 1–2 February 1955, shrimpboat YUKY); UCLA W55–23 (2:60.3, 111.6, Baja Calif., 1 mile S of San Felipe, 0–7 m, 9–11 March 1955, 600 ft

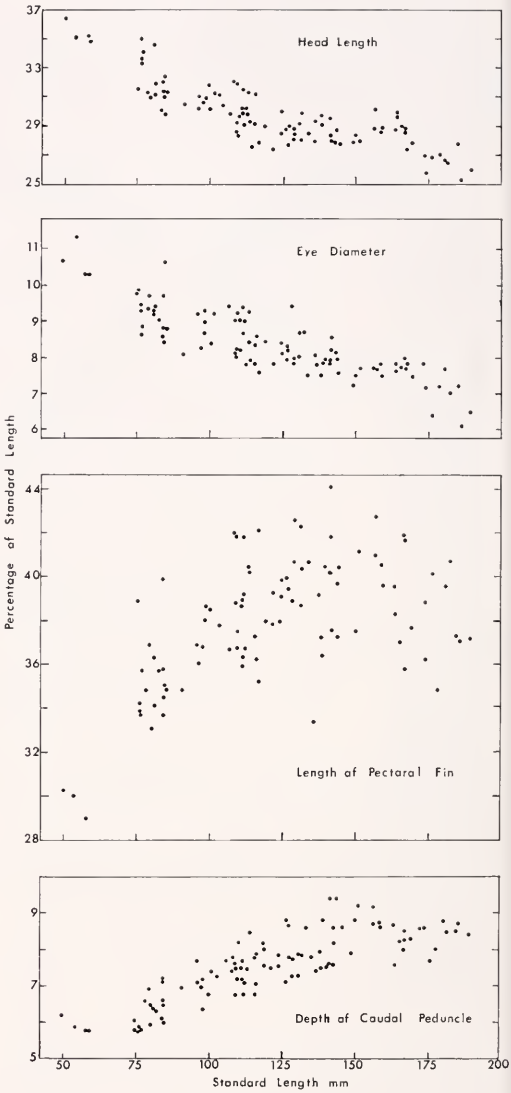


Figure 9. Ratio-on-size scatter diagrams for four morphometric characters of *Peprilus medius*.

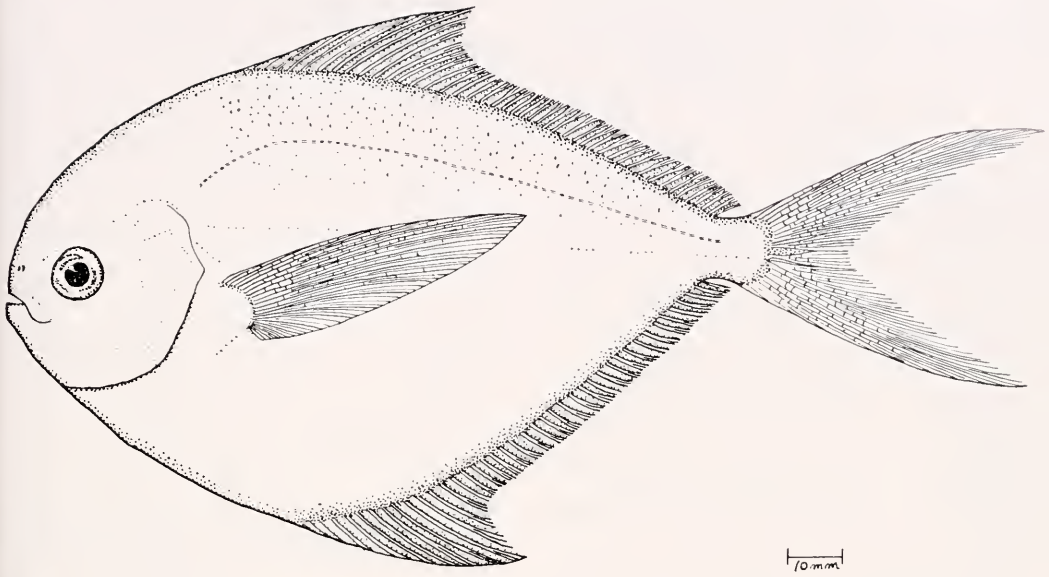


Figure 10. *Peprilus ovatus*, holotype, 128.7 mm SL, 20 miles SW of Golfo de Santa Clara, northern Gulf of California, USNM 203304.

beach seine); *UCLA W55–27 (6:56.2–110.6, Baja Calif., Punta Diggs, 5–10 miles S of San Felipe, 26 m, 11 March 1955, shrimpboat YUKY); *UCLA W55–28 (3: 112.7–132.0, Baja Calif., 4 to 5 miles N of San Felipe, 27 m, 11 March 1955, shrimpboat YUKY).

Diagnosis. *P. ovatus* is a short, deep-bodied species with slightly falcate dorsal and anal fins. It is distinguished from *P. snyderi* by having a much deeper body – mean body depth of 619 compared to 427 for *P. snyderi,* each in thousandths of SL; an eye diameter greater than the length of the snout; a mean number of dorsal fin-rays of 42.8 compared to 46.5 for *P. snyderi;* and 31 to 33 rather than 36 total vertebrae. It is distinguished from *P. simillimus* by having a much deeper body – mean body depth of 619 compared to 461 for *P. simillimus;* an eye diameter greater than the length of the snout; a mean number of anal fin-rays of 43.0 compared to 39.5 for *P. simillimus;* and 31 to 33 rather than 30 or 31 total vertebrae. Characters that distinguish *P. ovatus* from *P. medius* are listed in the diagnosis of the latter species. The specific epithet, *ovatus*, is from the Latin and is descriptive of the short, deep body of the species.

Description. Proportional measurements are given in Table 9 and meristic values in Table 10. Body ovate, deep, compressed; anterior dorsal profile moderately convex. Eye diameter greater than length of snout. Dorsal and anal fins slightly falcate, the longest dorsal ray three to six times the length of the shortest dorsal ray, the longest anal ray two to five times the length of the shortest anal ray. Dorsal fin with three or four (usually four) small, bladelike spines preceding the rays; anal fin with three or four (usually three) spines preceding the rays. Dorsal and anal fins originating at about the same level anteriorly, and the bases about equal in length. Caudal fin long to very long, deeply forked, about 24 to 35 per cent of total length. Lateral line of trunk highly arched

TABLE 9. PROPORTIONAL MEASUREMENTS OF *PEPRILUS OVATUS*. Symbols as in Table 7. Size range, 37.5–145.2 mm SL; mean size, 79.0 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	158	259–325	296	1.08	4.60
Snout length	158	052–074	063	0.39	7.75
Eye diameter	158	078–115	093	0.62	8.35
Length of upper jaw	158	065–094	080	0.43	6.75
Interorbital width	158	080–106	092	0.41	5.62
Length of pectoral fin	154	267–441	360	2.68	9.26
Predorsal distance I	158	369–465	408	1.52	4.67
Predorsal distance II	158	259–347	298	1.33	5.62
Preanal distance	158	427–552	481	2.13	5.57
Maximum depth of body	163	542–676	619	2.36	4.86
Least depth of caudal peduncle	158	060–094	079	0.54	8.59
In thousandths of HL:					
Snout length	158	176–244	213	1.23	7.23
Eye diameter	158	267–377	315	1.69	6.76
Length of upper jaw	158	234–313	271	1.20	5.55
Interorbital width	158	263–357	311	1.72	6.97

TABLE 10. MERISTIC VALUES OF *PEPRILUS OVATUS*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	145	40–46	42.8	0.12	3.27
Anal fin-rays*	147	40–46	43.0	0.12	3.40
Pectoral fin-rays	150	19–23	21.4	0.06	3.50
Total gill rakers	146	21–26	23.6	0.07	3.35
Total vertebrae	157	31–33	32.0	0.02	0.81
Lateral-line scales	–	–	–	–	–

* Excluding spines.

anteriorly, following dorsal profile posteriorly. Subdermal canal system visible as indistinct lines on the body; dendritic canals on top of head and nape often ill-defined. A series of medium-sized, irregularly-spaced, slitlike pores frequently visible along dorsal and upper ventral surfaces. Premaxillary teeth slightly recurved, pointed, and simple. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 200 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from about 4.6 to 9.3 (Table 9) and from 0.8 to 3.5 for meristic characters (Table 10). These values indicate that the relative dispersion of character values is nearly as great as that of its presumed closest relative, *P. medius*. It might be expected that such a species of restricted distribution would be less variable than that of the wide-ranging species from which it is derived.

The sample size is considered to be reasonably adequate. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all the species of *Peprilus*, is relatively constant (Table 5).

Geographic variation. No geographic variation was found in *P. ovatus* because of its apparently restricted distribution.

Ontogenetic change. Few and moderate changes accompany growth in *P. ovatus* in a size range of about 40 to 145 mm SL. With growth, eye diameter and head length decrease in size relative to SL, while the length of the pectoral fin and the depth of the caudal peduncle increase in size relative to SL (Fig. 11). The length of the pectoral fin, however, becomes nearly constant beyond about 100 mm SL. In contrast to the situation in the related *P. medius*, body depth in *P. ovatus* decreases in size relative to SL with growth (Fig. 12). The anterior lobes of the dorsal and

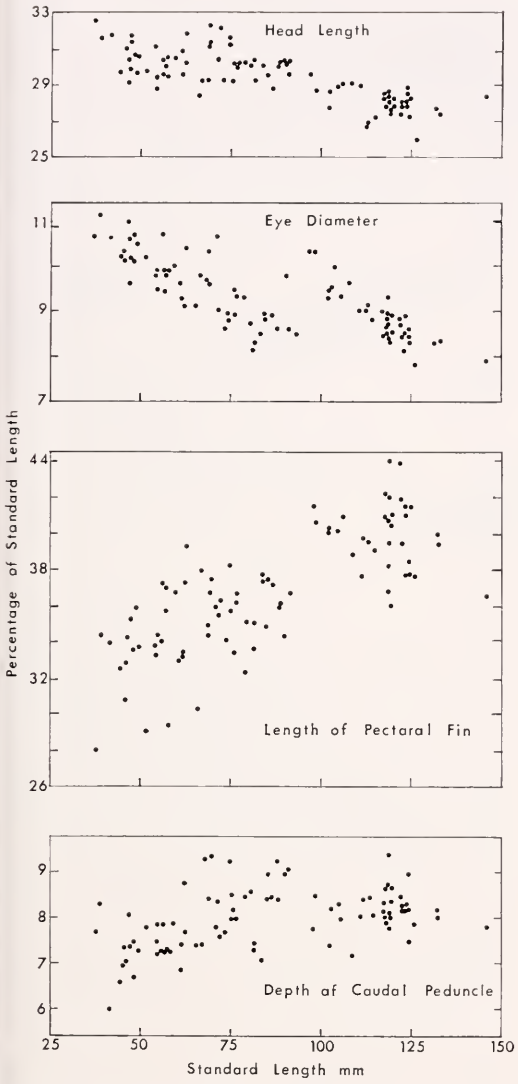


Figure 11. Ratio-an-size scatter diagrams for four morphometric characters of *Peprilus ovatus*.

anal fins tend to slightly increase in length with growth (compare Figs. 10 and 18b).

Distribution (Fig. 7). *P. ovatus* is known only from the northern Gulf of California from Punta Diggs south of San Felipe, Baja California, northward to the mouth of the Colorado River and from Golfo de Santa Clara, Sonora, to the mouth of the Colorado River.

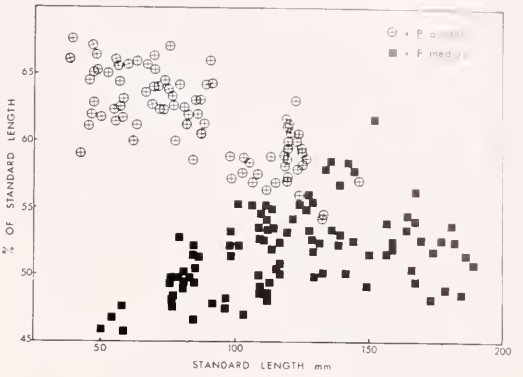


Figure 12. Ratio-an-size scatter diagram of body depth for *Peprilus medius* and *Peprilus ovatus*.

Taxonomic comments. See taxonomic comments under *P. medius*.

Peprilus simillimus (Ayres, 1860)
Figures 13, 18c

Poronotus simillimus Ayres, 1860: 84, fig. 1 (original description, San Francisco, California, holotype, a CAS specimen apparently destroyed by fire in 1906).

Stromateus simillimus, Jordan and Gilbert, 1881: 46; Jordan and Gilbert, 1882a: 451; Fordice, 1884: 314.

Rhombus (*Palometa*) *simillimus,* Jordan and Evermann, 1896: 967, *Palometa* erected as a subgenus.

Palometa simillima, Jordan and Evermann, 1898: 2849, subgenus *Palometa* elevated to generic level; Jordan, Evermann, and Clark, 1930: 266; Roedel, 1953: 81, fig. 78; Batts, 1960: 146, occurrence in Washington; Berry and Perkins, 1966: 673, distribution in California Current area; High, 1966: 53, fig. 1, occurrence in Puget Sound.

Peprilus simillimus, Clemens and Wilby, 1946: 201, fig. 38; J. L. Hart, 1949: 101; Haedrich, 1967: 107.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BC 62–242 (6:151.5–169.5 mm, British Columbia, Strait of Georgia, Pender Harbor and

Bargain Harbor, 4 radiographed); *BC 63–1447 (1:143.0, British Columbia, San Juan de Fuca Strait); CAS 1546 (1:168.5, San Francisco, Calif.); *CAS 1552 (1:157.0, San Francisco, Calif.); CAS 21929 (1:92.3, San Francisco Bay, Calif., 4 May 1955); *CAS 21943 (1:105.9, San Francisco Bay, Calif., 22 May 1955); *LACM 401 (11 meas.: 98.2–131.8, Calif., Los Angeles County, Long Beach, Belmont Shores, 25 October 1957, 58 radiographed); *LACM 3000 (1:76.2, Calif., Los Angeles Co., Long Beach, Belmont Shores, 19 October 1962); *LACM 21044 (1:68.2, Calif., Los Angeles Co., Venice Pier, 15 August 1914); MCZ 16885 (2:118.0, 121.5, San Francisco, Calif.); MCZ 17337 (1:192.5, San Francisco, Calif.); MCZ 23394 (1:202.0, San Francisco, Calif.); MCZ 23395 (1:168.0, San Francisco, Calif.); MCZ 23399 (1: 174.0, San Francisco, Calif.); *SIO H52–221 (4:28.4–49.8, Pacific Ocean, Baja Calif., San Martin I., Hassler Cove, found in bell of jellyfish, *Pelagia* sp., 14 September 1952, 1 radiographed, 1 CS); *SIO 59–70 (1:71.0, Pacific Ocean, Baja Calif., 26°48′N, 113°25′W, 3 July 1958); *SIO 60–394 (1:86.4, Pacific Ocean, Baja Calif., Sebastián Vizcaíno Bay, 28°34.5′N, 114°24′W, 19 August 1960); *SIO 60–409 (1:48.0, Calif., San Diego Co., La Jolla Bay, found in bell of jellyfish, *Pelagia* sp., 6 July 1960); *SIO 62–236 (1:137.5, Gulf of Calif., Baja Calif., Bahía de Los Angeles, 28°55′–56′N, 113°31′–33′W, 20 m, 26 April 1962); *SIO 62–580 (1:68.7, Calif., Imperial Co., on beach at Salton Sea, apparently a live-bait transfer, 3 September 1962); *SIO 62–681 (20 meas.:78.7–144.9, Calif., off San Diego, 32°46.5′N, 117°18.5′–19.7′W 0–82 m, 1 September 1962, R/V JOHN N. COBB, Cobb Mark II pelagic trawl, 23 radiographed); *SIO 64–641 (5:107.4–129.0, Pacific Ocean, Baja Calif., E of Cedros I., 2 miles from shore, 15 m, 17 August 1961); *SIO 64–747 (2:78.2, 86.0, Pacific Ocean, Baja Calif., Bahía Magdalena, from bait sample, 7 September 1954, M/V MARY C. CANAS); *SU 4382 (6:96.3–158.5, Monterey Bay, Calif.); SU 48000 (1:85.0, off Oceanside, Calif., 17 November 1943); *USNM 4472 (1:172.0, San Francisco, Calif.); *USNM 26800 (4:101.0–143.0, San Diego, Calif.); *USNM 26910 (4:113.0–144.0, Santa Barbara, Calif.); *USNM 38015 (1:108.0, San Diego, Calif.); *USNM 42045 (2:135.4, 150.0, Wash., Seattle market); *USNM 52998 (1:168.0, Calif., San Pedro market); *UCLA W56–360 (4: 79.0–96.4, Pacific Ocean, Baja Calif., Turtle Bay, 27°41′N, 114°53′W, 0–7 m, 22 July 1956, bait net); *UW 13405 (4:140.3–153.3, Wash., Strait of Georgia, Bellingham Bay, 8 February 1946); *UW 14656 (9:164.7–198.0, Wash., Puget Sound, Fletcher Bay, 11 December 1959); *UW 18210 (6:119.3–152.4, Wash., Orcas I., East Sound, 0–27 m, 10 September 1963).

Diagnosis. *P. simillimus* is an elongate, shallow to moderately deep species with only slightly falcate dorsal and anal fins. The species is distinguished from *P. snyderi* by having a mean number of dorsal fin-rays of 44.8 compared to 46.5 for *P. snyderi;* a mean number of anal fin-rays of 39.5 compared to 42.0 for *P. snyderi;* and 30 or 31 rather than 36 total vertebrae. Characters that distinguish *P. simillimus* from *P. medius* and *P. ovatus* are listed in the diagnosis of each of these species, respectively. *P. simillimus* is distinguished from the similar *P. triacanthus* by having no row of relatively large pores beneath the anterior half of the dorsal fin. The specific epithet, *simillimus,* is from the Latin, "similis," meaning like or resembling; the species was so named because of its similarity to *P. triacanthus.*

Description. Proportional measurements are given in Table 11 and meristic values in Table 12. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly convex. Eye diameter about equal to the length of the snout; eye relatively small. Dorsal and anal fins slightly falcate, the longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the

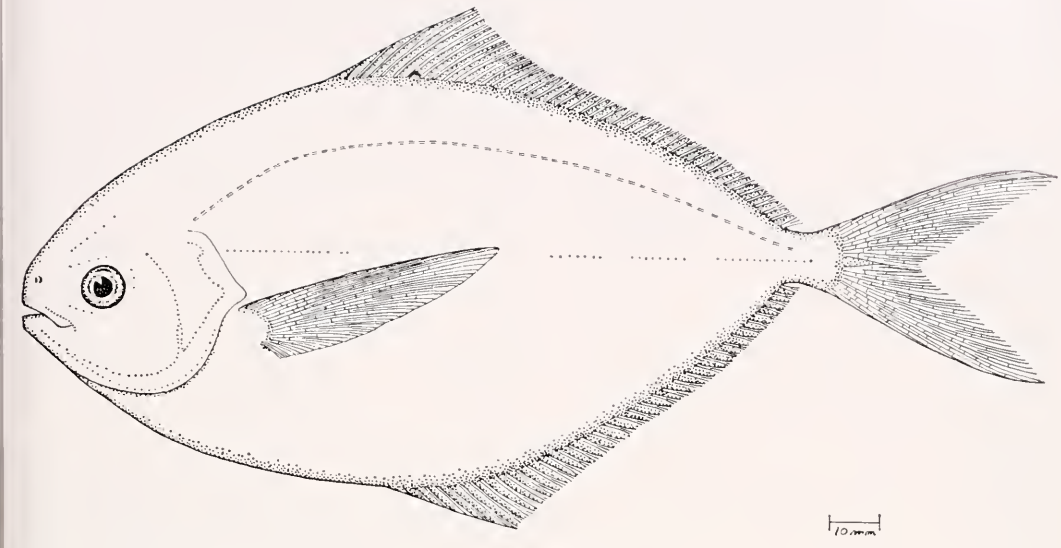


Figure 13. *Peprilus simillimus*, 164.7 mm SL, Puget Sound, Washington, UW 14656.

length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) spines anterior to the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long, moderately to deeply forked, about 18 to 32 per cent of total length. Subdermal canal system visible as indistinct parallel lines on body in preserved material; dendritic canals on top of head and nape distinct. Premaxillary teeth slightly recurved, mostly pointed, simple, but a few on a particular specimen may have two or three small cusps. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Except for eye diameter, coefficients of variation (V) for proportional measurements range from 3.8 to about 9 (Table 11) and from 1.2 to 4.2 for meristic characters (Table 12). The V value for eye diameter as a percentage of SL is 17.44, a high value resulting from allometric growth.

The sample size (Table 11) of *P. simillimus* used is considered to be reasonably adequate, and specimens from almost all parts of the known range have been examined. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all species of *Peprilus*, is relatively constant (Table 5).

Geographic variation. There is slight but inconclusive evidence that northern members of *P. simillimus* are larger and deeper-bodied. The dorsal, anal, and caudal fins of northern specimens seem to be shorter and less conspicuous. The differences are slight in the dorsal and anal fins, but more prominent in the caudal fin. Length of the caudal fin expressed as a percentage of the total length in specimens from San Francisco to British Columbia is less on the average than in specimens taken from Monterey to Baja California (Fig. 14). Although the ranges of the two groups overlap, the difference in the means is highly significant with a probability of much less than 0.001 using a two-tailed Student's *t*-test.

The functional significance of shorter or lower fin lobes in northern populations of fish species is apparently unknown. Per-

Table 11. Proportional Measurements of *Peprilus simillimus*. Symbols as in Table 7. Size range, 28.4–202.0 mm SL; mean size, 123.8 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	109	252–408	285	2.28	8.35
Snout length	109	058–081	070	0.45	6.74
Eye diameter	109	050–119	073	1.22	17.44
Length of upper jaw	109	064–100	076	0.64	8.82
Interorbital width	109	076–110	089	0.53	6.26
Length of pectoral fin	109	272–379	336	2.28	7.41
Predorsal distance I	103	338–407	369	1.37	3.76
Predorsal distance II	109	222–339	263	1.82	7.23
Preanal distance	109	402–518	440	2.01	4.78
Maximum depth of body	109	394–517	461	2.01	4.57
Least depth of caudal peduncle	109	055–074	065	0.43	6.83
In thousandths of HL:					
Snout length	109	192–287	246	2.11	8.95
Eye diameter	109	188–347	255	2.62	10.71
Length of upper jaw	109	218–323	267	1.63	6.39
Interorbital width	109	259–369	314	2.07	6.89

haps the difference is allied to differential growth rates as influenced by regional conditions of temperature. The shorter fin lobes may possibly be associated with surface-volume ratios and with adaptations to cooler temperatures.

Ontogenetic change. Few and moderate changes accompany growth in *P. simillimus* in a size range of about 28 to 202 mm SL. With growth, head length and eye diameter decrease in size relative to SL while depth of body and of caudal peduncle remain nearly constant (Fig. 15). The correlation coefficient of the size-on-size regression of eye diameter is the lowest among members of the genus (Fig. 3; Table 6). The length of the pectoral fin increases slightly in size relative to SL with growth up to about 125 mm SL, beyond which there is a slight decrease (Fig. 15).

Table 12. Meristic Values of *Peprilus simillimus*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	98	41–48	44.8	0.16	3.50
Anal fin-rays*	100	35–44	39.5	0.15	3.67
Pectoral fin-rays	107	19–23	21.1	0.06	3.13
Total gill rakers	75	23–26	23.9	0.12	4.18
Total vertebrae	160	30–31	30.2	0.03	1.19
Lateral-line scales	9	95–110	–	–	–

* Excluding spines.

Distribution (Fig. 7). *P. simillimus* is known along the Pacific Coast of North America from southern Baja California to southern British Columbia. The southern limit of the range is in the vicinity of Bahía Magdalena, Baja California, at about 24°30′N. One specimen here referred to as *P. simillimus* is known from the Gulf of California: a female, 137.5 mm SL, from Bahía de Los Angeles, Baja California, 28°55′–56′N, 113°31′–33′W (SIO 62–236). The northern known extents of the range are near Clayoquot Sound on the west Coast of Vancouver Island, near Nanaimo on the east coast of the Island, and near the mouth of the Fraser River at Vancouver, British Columbia, all at about 49°N.

Taxonomic comments. Ayres (1860) in his original description of this species placed it "with doubt" in the genus *Poronotus*, noting that it lacked the relatively large dorsal pores characterizing *Poronotus triacanthus*. Until he received Gill's (1861) "Catalogue of the fishes of the eastern coast of North America from Greenland to Georgia," Ayres had recorded the new

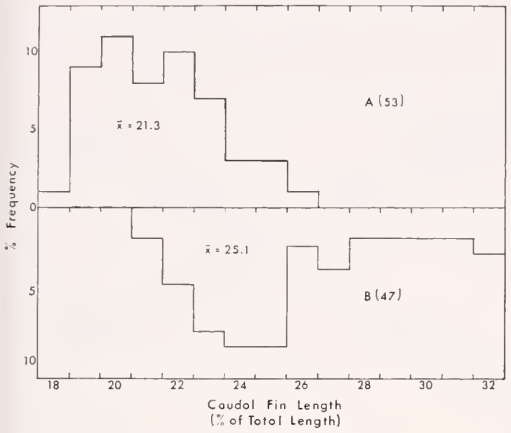


Figure 14. Geographic variation of caudal fin length in *Peprilus simillimus*: A = specimens collected between British Columbia and San Francisco; B = specimens collected between Monterey, California, and southern Baja California; numbers in parentheses are the sample sizes; $\bar{x}$ = mean. The means are highly significantly different at the 2 per cent level (two-tailed Student's *t*-test).

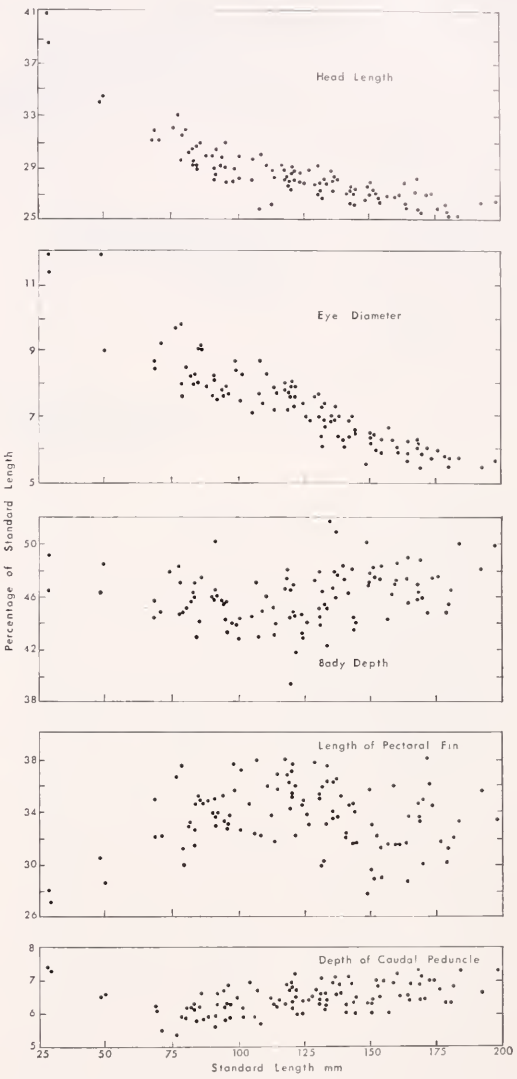


Figure 15. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus simillimus*.

species in his manuscript notes as *Peprilus simillimus*. Since Gill reserved the genus *Peprilus* for the deep-bodied species with falcate median fins, and the genus *Poronotus* for the elongate species with relatively large dorsal pores, Ayres with reluctance placed the new species in the genus *Poronotus* because of the overall similarity to *Poronotus triacanthus*.

This species is often referred to in faunal and fishery works as *Palometa simillima*, after Jordan and Evermann's (1898) designation.

The common names of *P. simillimus* on the Pacific Coast, "California pompano," "Pacific pompano," or "pompano," are somewhat misleading since "pompano" is most frequently used in reference to certain fishes of the family Carangidae. A more appropriate name might be "Pacific butterfish" after the familiar butterfish, *P. triacanthus*, of the Atlantic Coast.

Peprilus snyderi Gilbert and Starks, 1904 Figures 16, 18d

Peprilus snyderi Gilbert and Starks, 1904: 87, fig. 23, pl. XII (original description, Panama Bay, holotype not seen; three paratypes seen, 2:188.0, 193.0 mm SL. SU 7009; 1:182.3, USNM 50448); Meek and S. F. Hildebrand, 1925: 413; Haedrich, 1967: 107.

Palometa snyderi, Jordan, Evermann, and Clark, 1930: 267.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless other-

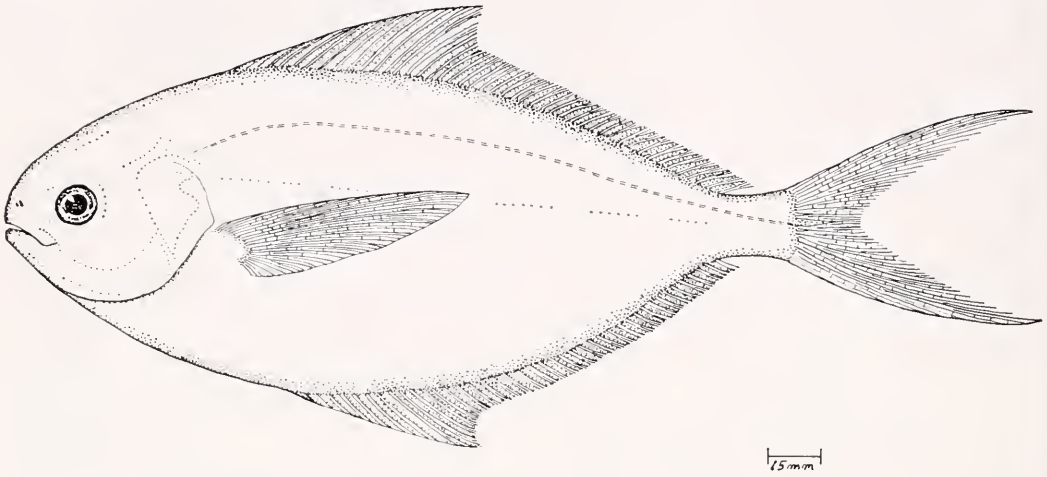


Figure 16. *Peprilus snyderi*, 227.0 mm SL, Acapulco market, Mexico, BC 61-126.

wise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BC 59–247 (1:205.0 mm, Mazatlán, Mexico); *BC 59–687 (3:190.0–213.0, Panama City market); *BC 60–25 (1:193.0, Mex., Golfo de Tehuantepec, Puerto Arista to Salina Cruz); *BC 61–126 (1:227.0, Mex., Acapulco market); *FMNH 73840 (1:227.0, Mex., 1–5 miles off Chiapas coast at Guatemala border to above San Benito, 18–27 m, 14–18 December 1954); IMS 1310 (1:143.6, Mex., Salina Cruz market, 16 August 1963); *LACM 8859–2 (3: 152.5–159.2, Gulf of California, 24°29′N, 110°26′W, 0–15 m captured in 82–110 m water, 6 April 1964, R/V ALASKA); *SIO H50–181 (3:238.0–245.0, Pacific Ocean, Baja Calif., Bahía San Juanico, San Juanico Anchorage, 26°15′N, 112°28′W, 12 April 1950, snag hooks); *SU 7009 (2:188.0, 193.0, paratypes, Panama Bay); *USNM 50448 (1:182.3, paratype, Panama Bay); *UCLA W53–267 (1:232.0, Panama City market, 23 June 1953); *UCLA W55–23 (1:179.0, Gulf of Calif., Baja Calif., 1 mile S of San Felipe, 0–7 m, 9–11 March 1955, 600 ft beach seine); *UCLA W56–113 (1: 121.2, Gulf of Calif., Sinaloa, Mex., just S of mouth of Bahía Topolobampo, 6–11 m, 24 May 1956); *UCLA W56–129 (4:42.1–65.7, Jalisco, Mex., Bahía de Banderas, 20°32′N, 105°17′W, 0–7 m, 18 March 1956, bait net, 1 CS).

Diagnosis. *P. snyderi* is an elongate, wide-ranging, rarely-collected species with slightly falcate dorsal and anal fins. Characters that distinguish *P. snyderi* from *P. medius*, *P. ovatus*, and *P. simillimus*, are listed in the diagnosis of each of these species, respectively.

Description. Proportional measurements are given in Table 13 and meristic values in Table 14. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly convex. Eye diameter about equal to the length of the snout; eye relatively small. Dorsal and anal fins slightly falcate, the longest dorsal ray three to five times the length of the shortest dorsal ray, the longest anal ray two to five times the length of the shortest anal ray. Dorsal and anal with two or three (usually three) small spines preceding the rays; spines appear to be somewhat smaller and less conspicuous than in other members of the genus. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long, moderately to deeply forked, about 20 to 30 per cent of total length. Scales

Table 13. Proportional Measurements of *Peprilus snyderi*. Symbols as in Table 7. Size range, 42.1–245.0 mm SL; mean size, 170.0 mm SL.

	N	R	$\bar{x}$	SE	V
In thousandths of SL:					
Head length	24	262–380	297	6.97	11.50
Snout length	24	059–083	068	1.23	8.85
Eye diameter	24	057–103	070	2.83	19.80
Length of upper jaw	24	066–107	081	2.17	13.14
Interorbital width	24	079–104	087	1.14	6.43
Length of pectoral fin	22	289–361	329	3.34	4.78
Predorsal distance I	24	332–430	364	6.18	8.32
Predorsal distance II	24	224–315	253	5.79	11.22
Preanal distance	24	367–505	424	7.38	8.53
Maximum depth of body	24	371–503	427	7.35	8.43
Least depth of caudal peduncle	24	050–082	071	1.75	12.10
In thousandths of HL:					
Snout length	24	191–250	230	2.84	6.05
Eye diameter	24	209–279	234	4.40	9.21
Length of upper jaw	24	250–290	272	1.96	3.53
Interorbital width	24	217–322	295	5.19	8.62

Table 14. Meristic Values of *Peprilus snyderi*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	24	43–49	46.5	0.28	2.88
Anal fin-rays*	23	40–44	42.0	0.30	3.35
Pectoral fin-rays	22	21–23	22.3	0.15	3.14
Total gill rakers	18	23–26	24.1	0.24	4.23
Total vertebrae	23	36	36.0	0.00	0.00
Lateral-line scales	12	110–130	–	–	–

* Excluding spines.

apparently somewhat less deciduous than in other members of the genus. Subdermal canal system visible as indistinct parallel lines on body in preserved material; dendritic canals on top of head and nape distinct. Premaxillary teeth slightly recurved, mostly pointed, simple, but a few on a particular specimen may have two or three small cusps. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 300 mm SL.

Variation. Except for eye diameter, coefficients of variation (V) for proportional measurements range from 3.5 to 13.1 (Table 13). The V values for meristic characters range from 2.9 to 4.2, excluding vertebral number which showed no variation (Table 14). The V value for eye diameter as a percentage of SL is 19.8. This range of V values is wider than for other species and may be at least partially explained by the small sample size (24), which consisted of several large fish and a few small fish.

Geographic variation. No geographic variation was noted in this species.

Ontogenetic change. Few and moderate changes accompany growth in *P. snyderi* although the sample, 24 specimens between 42 and 245 mm SL, was small and lacked individuals between 60 and 120 mm. With growth, head length, eye diameter, and body depth decrease in size relative to SL while the relative depth of the caudal peduncle increases slightly and the relative length of the pectoral fin remains nearly constant (Fig. 17).

Distribution (Fig. 7). *P. snyderi* is known along the Pacific Coast from Panama Bay northward to the upper part of the Gulf of California near San Felipe (about 31°N) and to Bahía San Juanico (about 26°15′N) on the outer coast of Baja California. Collections from intermediate localities are few, but the species probably occurs along this entire coastal region.

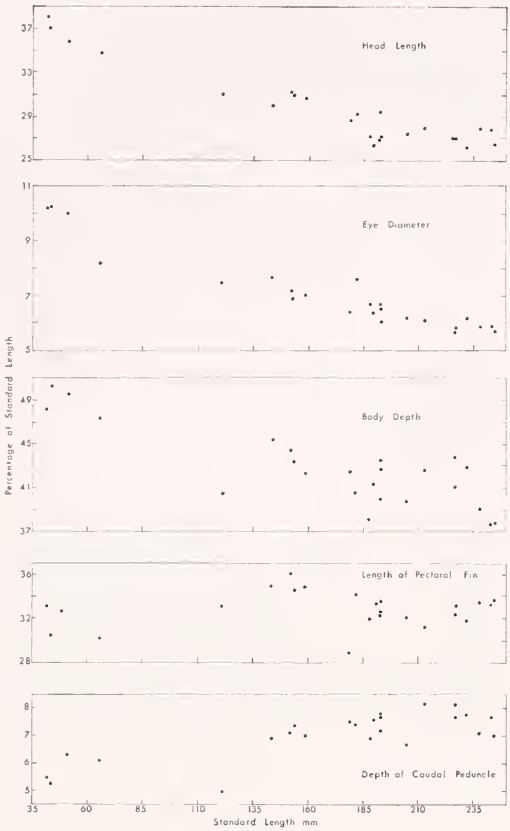


Figure 17. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus snyderi*.

Peprilus burti Fowler, 1944
Figures 19, 31

Poronotus triacanthus (not of Peck, 1804), Fowler, 1933: 61, Breton Island, Louisiana (misidentification); Briggs, 1958: 292, in part, Gulf of Mexico populations; Caldwell, 1961: 19, pl. 10, in part, bottom fish in photograph, Gulf of Mexico *Peprilus burti* synonymized with Atlantic *Poronotus triacanthus*.

Peprilus burti Fowler, 1944: 1, fig. 1 (original description, Breton Island, Louisiana, holotype seen, 113.3 mm SL, ANSP 55841; five paratypes seen, 2:73.3, 82.0, ANSP 55842–55843; 3:66.5–71.5, Galveston, Texas, ANSP 70943–70945); Haedrich, 1967: 108.

Poronotus burti, Collette, 1963: 582, valid species based on vertebral number.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). All localities are in the Gulf of Mexico. *ANSP 55841 (1:113.3 mm, holotype of *Peprilus burti* Fowler, 1944, Breton I., Louisiana, November, 1930); *ANSP 55842, 55843 (2:73.3, 82.0, paratypes of *Peprilus burti* Fowler, 1944, Breton I., La., November, 1930); *ANSP 70943 to 70945 (3:66.5–71.5, paratypes of *Peprilus burti* Fowler, 1944, Galveston, Texas, 1943); FSBC 372 (10:34.4–47.3, Florida, Escambia County, E of Pensacola Bay Bridge, 1 February 1958); FSBC 1640 (1:44.5, Fla., Pinellas Co., Madeira Beach, February, 1960); FSBC 2283 (6:96.2–106.1, Mississippi, Horn I., 27 October 1962); FSBC 3211 (1:63.6, Fla., Tampa Bay, grass flats, 9 October 1964); FSBC 3832 (1:71.2, Fla., Tampa Bay, 23 February 1966); FSBC 3954 (1:86.0, Fla., Pinellas Co., 27 December 1966, R/V CORTEZ); IMS 324 (1:80.5, Tex., Green Bayou, 11–15 m, 23 October 1950); IMS 327 (1:24.8, Port Aransas, Tex., from *Stomolophus* medusa, 27 November 1950; 1:28.2, Port Aransas, Tex., tide trap, 16 June 1950; 2:29.5, 30.0, Port Aransas, Tex., Humble Docks, dipnet, 1 May 1948); IMS 328 (5:79.0–88.8, 60–70 miles S of Port Aransas, Tex., 33–42 m, 13–16 May 1951); IMS 329 (1:120.8, 100 miles S of Port Isabel, Tex., 57–68 m, 6–11 March 1951; 2:82.5, 109.0, 40–60 miles S of Port Aransas, Tex., 22–33 m, 6–11 July 1951); IMS 330 (1:122.6, Mexico, Punta Frontera, 24–37 m, 29 July to 7 August 1951; 1:128.8, Tex., Corpus Christi Pass, 33–42 m, 22–23 January 1951); IMS 981 (3:100.8–107.9, Port Aransas, Tex., 37 m, 24 July 1962); IMS 1179 (3:98.7–105.3, Port Aransas, Tex., 10 July 1962); IMS uncat. (8:28.4–88.4, Port Aransas, Tex., spring, 1964); *MCZ 35118 (4:68.0–76.0, Pensacola, Fla.); MCZ 41924 (4:6.7–9.0, 28°51′N, 88°37′W, at surface over 695 m, M/V OREGON Sta. 852, 25 October 1953, 2 CS); MCZ 45015 (10:

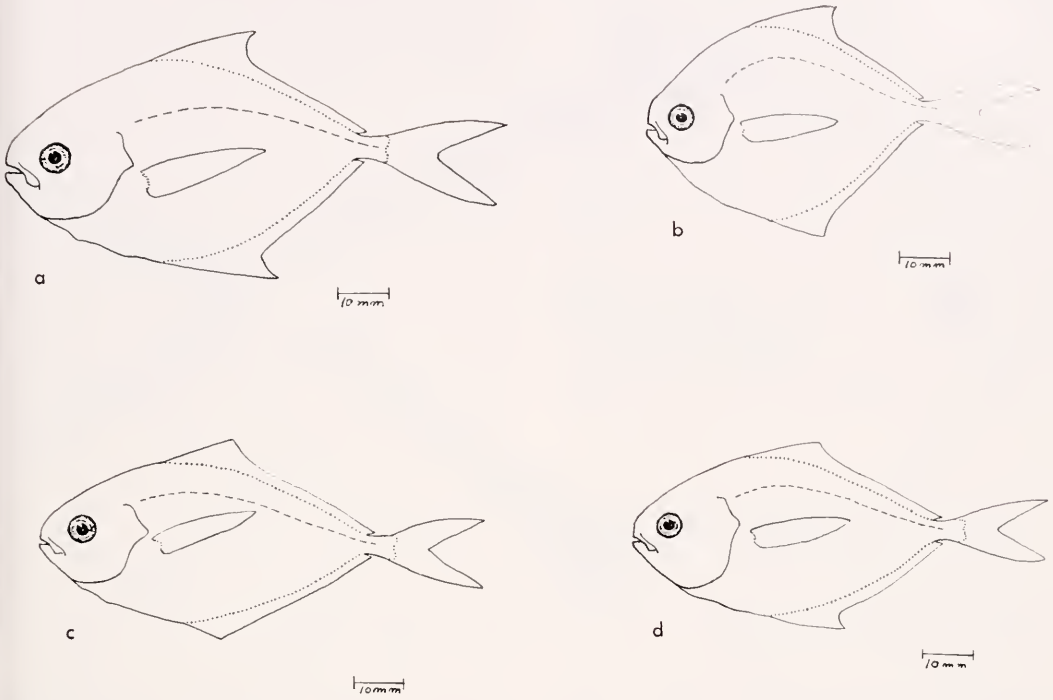


Figure 18. Juveniles of the four Pacific species of *Peprilus*: a = *P. medius*, 77.9 mm SL; b = *P. ovatus*, 60.0 mm SL; c = *P. simillimus*, 71.0 mm SL; d = *P. snyderi*, 66.4 mm SL.

113.5–136.0, 29°45′N, 88°20′W, 37 m, M/V SILVER BAY Sta. 296, 12 March 1958); *MCZ uncat. (22:55.6–102.2, Port Aransas, Tex., 7–20 m, R/V LORENE, 30 June 1967, 16 radiographed); TABL uncat. (1:136.4, 27°04′N, 96°43′W, 82 m, M/V SILVER BAY Sta. 266, 28 January 1958); TABL uncat. (1:133.5, 20°01′N, 91°47′W, 55 m, M/V SILVER BAY Sta. 844, 17 November 1958); TABL uncat. (4:44.0–52.0, Fla., lower Pensacola Bay, between ship channel and south shore from Big Lagoon entrance to U. S. Coast Guard Station, 20 February 1964); TABL uncat. (1:133.7, Fla., 45 miles SW of Pensacola); TU 3979 (3:86.0–104.5, La., Terrebonne Co., Oyster Bayou, 2–4 m, 31 May 1952); TU 4084 (10:38.5–56.2, La., Terrebonne Co., Oyster Bayou 4 m, 12 March 1952); TU 4461 (10:12.5–17.5, La., Jefferson Co., NE end of Grand I., 2–3 May 1952); TU 8945 (7:78.7–122.9, La., Miss. Sound near Grand I. channel, 30°09′N, 89°18′W, M/V ANN INEZ, 26 August 1954); TU 23966 (10: 16.3–30.6, 29°50.5′N, 85°32.5′W, 22 m, M/V OREGON Sta. 2431, 4 March 1959); *USNM 118620 (4:72.0–79.0, Aransas Pass, Tex., 12 May 1940); USNM 147777 (1: 109.0, Miss., 1948); USNM 156116 (1: 100.0, La., Grand I., Barataria Bay, 5 July 1930); *USNM 156118 (2:88.0, 91.0, La., Barataria Bay, 27 November 1951); USNM 156121 (1:97.0, La., Grand I., 5–8 m, 2 July 1930); USNM 156122 (1:97.0, La., Grand I., 21 July 1930); *USNM 156123 (5:94.0–107.0, La., Grand I., 12 miles off Grand Terre, 22 July 1930); *USNM 156124 (1:86.0, Fla., Appalachicola Bay, June, 1932); *USNM 157709 (2:99.0, 100.0, Alabama, 9 m, 29 September 1951); *USNM 159714 (3:56.0–73.0, 30°12.5′N, 88°15′W, Ala., 11 m, M/V OREGON Sta.

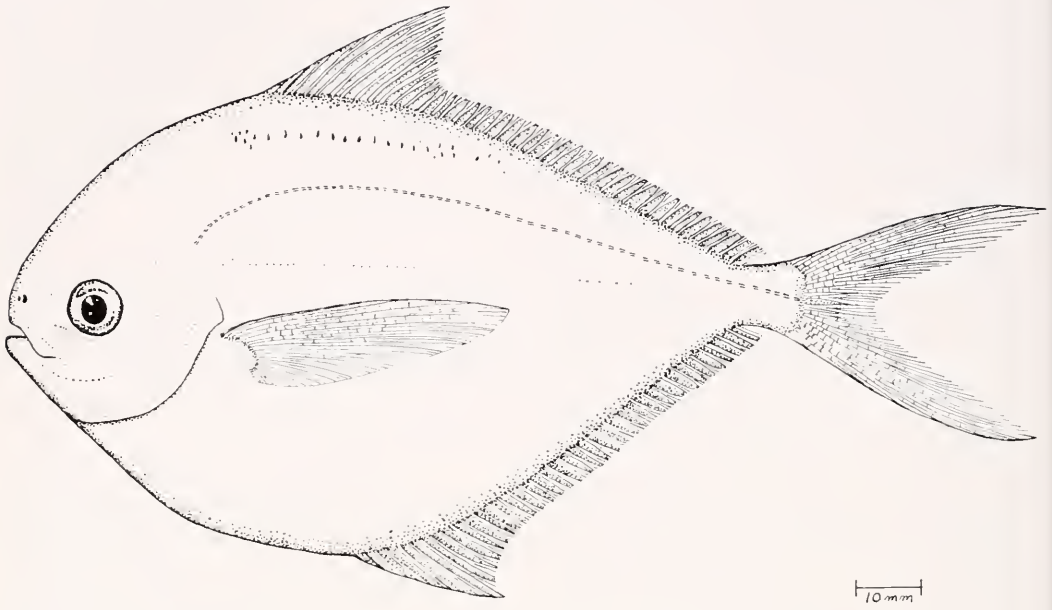


Figure 19. *Peprilus burti*, 113.7 mm SL, Mississippi Sound, 30°09′N, 89°18′W, TU 8945.

2142, 12 March 1958); *USNM 159808 (1:145.0, 28°58′N, 84°44′W, 144 m, M/V SILVER BAY Sta. 154, 22 August 1957); USNM 159825 (1:123.1, 28°30′N, 94°97′W, 35 m, M/V SILVER BAY Sta. 187, 25 September 1957); USNM 163517 (1:143.0, 28°09′N, 84°54′W, 146 m, M/V OREGON Sta. 920, 11 March 1954); *USNM 187922 (4:142.0–167.0, 29°04′N, 85°49′W, 183–186 m, M/V SILVER BAY Sta. 156, 22 August 1957); *USNM 187924 (1:54.2, 29°42′N, 88°40′W, 15–18 m, M/V OREGON Sta. 2193, 25 May 1958); *USNM 187987 (6 meas.:69.0–93.0, 29°07′N, 88°34′W, 229 m, M/V OREGON Sta. 3646, 14 June 1962, 11 radiographed); USNM 188649 (2:103.0, 104.0, 28°47′N, 91°49.5′W, 26 m); USNM uncat. (4:32.0–63.0, 30°09′N, 88°29′W, 13 m, M/V OREGON Sta. 2115, 24 February 1958); *USNM uncat. (3:58.0–76.0, 30° 12.5′N, 88°15′W, 11 m, M/V OREGON Sta. 2142, 12 March 1958); *USNM uncat. (31 meas.:53.9–102.1, 30°02′N, 88°42.5′W, 15–17 m, M/V OREGON Sta. 2389, 29 January 1959, 103 radiographed, 2 CS); *USNM uncat. (10:132.0–155.0, Yucatan Peninsula, W of Campeche, 19°42′N, 91° 47′W, 49–55 m, M/V SILVER BAY Sta. 1131, 25 April 1959); UMML 750 (4:53.5–68.4, Fla., Appalachicola Bay, 1951); UMML 1804 (1:61.3, Yucatan Peninsula, Campeche, SW of Monas Pt.); UMML 11002 (1:130.8, 28°13.5′N, 92°56′W, 68 m, M/V OREGON Sta. 3804, 14 September 1962); UMML 13268 (1:83.3, 30°07.5′N, 88°42.5′W, 16 m, M/V SILVER BAY Sta. 5006, 22 June 1963); UMML 15813 (1: 65.9, 30°07.5′N, 88°43′W, 15 m, M/V SILVER BAY Sta. 5007, 22 June 1963).

Diagnosis. *P. burti* is a moderately elongate species with slightly falcate dorsal and anal fins. It is distinguished from the closely related *P. triacanthus* by having a deeper body – a mean body depth of 551 compared to 458 for *P. triacanthus*, each in thousandths of SL; 16 or 17 rather than 18 to 20 caudal vertebrae; and, no dark spots along dorsal surface as are frequently present in *P. triacanthus*. The species is distinguished from *P. paru* by having a

Table 15. Proportional Measurements of *Peprilus burti*. Symbols as in Table 7. Size range, 7.8–167.0 mm SL; mean size, 79.5 mm SL.

	N	R	$\bar{x}$	SE	V
In thousandths of SL:					
Head length	216	255–392	303	1.78	8.66
Snout length	215	048–096	069	0.58	12.26
Eye diameter	229	065–144	100	0.97	14.68
Length of upper jaw	215	074–128	089	0.63	10.39
Interorbital width	215	059–131	097	0.65	9.88
Length of pectoral fin	219	228–391	332	3.03	13.49
Predorsal distance I	205	331–529	395	2.59	9.39
Predorsal distance II	215	239–448	292	2.72	13.66
Preanal distance	215	404–582	465	2.38	7.52
Maximum depth of body	232	460–640	551	2.45	6.76
Least depth of caudal peduncle	215	050–096	075	0.52	10.08
In thousandths of HL:					
Snout length	215	167–278	226	1.28	8.31
Eye diameter	216	251–424	328	2.32	10.40
Length of upper jaw	215	200–371	295	1.47	7.33
Interorbital width	214	200–411	319	2.02	9.29

Table 16. Meristic Values of *Peprilus burti*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	155	38–48	43.6	0.12	3.53
Anal fin-rays*	155	35–43	39.7	0.11	3.35
Pectoral fin-rays	148	19–23	21.4	0.06	3.59
Total gill rakers	71	21–26	23.3	0.11	3.91
Total vertebrae	273	29–31	30.0	0.01	0.67
Lateral-line scales	4	90–100	–	–	–

* Excluding spines.

row of relatively large pores below the anterior half of the dorsal fin, and by having slightly falcate dorsal and anal fins rather than moderately or extremely falcate ones.

Description. Proportional measurements are given in Table 15 and meristic values in Table 16. Body moderately elongate, moderately deep to deep, compressed; anterior dorsal profile moderately convex. Eye diameter greater than length of snout; eye relatively large. Dorsal and anal fins slightly falcate, longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal fin (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. The system is often very conspicuous in living or freshly collected specimens. There is an irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. Premaxillary teeth slightly recurved, usually with three small cusps. Swimbladder delicate, thin-walled, elongate; found only in specimens smaller than about 100 mm SL. Coloration as described for the genus. Maximum length probably 200 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 6.8 to 14.7 (Table 15) and from 0.7 to 3.9 for meristic characters (Table 16). Comparatively high V values for proportional measurements result partly from some degree of allometry, especially in eye size, and from the inclusion in the sample of a wide size-range of individuals.

The sample size of *P. burti* used (Table

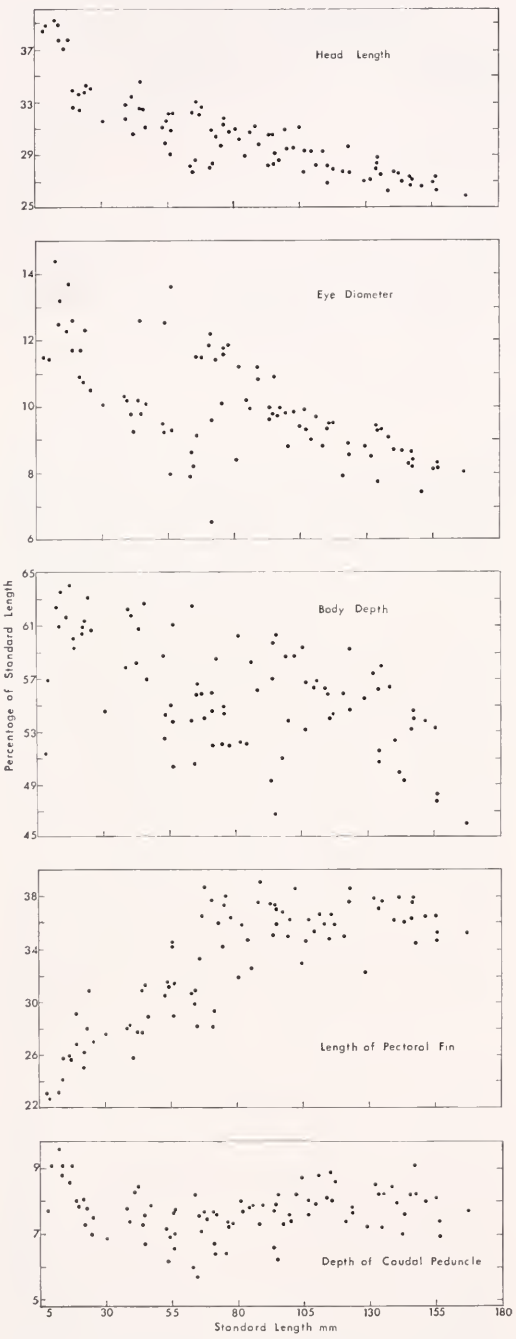


Figure 20. Ratio-on-size scatter diagrams for five marphometric characters of *Peprilus burti*.

15) is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). The main exception is vertebral number which, as in all the species of *Peprilus*, is relatively constant (Table 5).

Geographic variation. No geographic variation was noted in this species.

Ontogenetic change. Few and moderate changes accompany growth in *P. burti* in a size range of about 8 to 167 mm SL. As shown by ratio-on-size diagrams (Fig. 20), head length, eye diameter, and body depth decrease in size relative to SL with growth, while the relative length of the pectoral fin increases up to about 100 mm SL then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient of the size-on-size regression of eye diameter is relatively low (Fig. 3; Table 6). The size-on-size regressions of body depth for *P. burti* and the closely related *P. triacanthus* (Fig. 2) show the two to be similar in this character up to about 30 mm SL, beyond which size *P. burti* becomes deeper-bodied.

Distribution (Fig. 7). *P. burti* is known only from the Gulf of Mexico. The range extends from the vicinity of Tampa Bay, Florida (about 27°45′N), along the continental shelf to the western side of Yucatan, Mexico (about 21°45′N). Caldwell (1961) lists two records for the species outside of the above range: 1) Big Sarasota, Florida, about 27°30′N, CAS 17237; and 2) Cape Romano, Florida, about 25°54′N, M/V SILVER BAY Sta. 524, the latter based on an unsupported field report. Specimens agreeing closely to the description of *P. burti* are known from shallow water in the Atlantic off Florida. These specimens may represent disjunct members of the species. All such specimens are, however, listed under *P. triacanthus*, the closely related Atlantic Coast species.

Taxonomic comments. *P. burti* was originally described as a new species by Fowler (1944) from specimens which he had previously (1933) designated as Gulf of Mexico members of *Poronotus triacanthus*. Fowler (1944) stated that the species was apparently related to *Peprilus palometa* of the Pacific Coast even though he recognized that the former species was different in several respects, including the possession of a row of relatively large pores below the dorsal fin.

P. burti is very closely related to *P. triacanthus* of the Atlantic Coast, a relationship resulting in different interpretations of taxonomic status. Populations in the Gulf of Mexico are frequently referred to as *Peprilus* or *Poronotus triacanthus*. Caldwell (1961) proposed the synonymy of *Peprilus burti* with *Poronotus triacanthus*. Collette (1963), on the basis of differing vertebral counts, considered *P. burti* to be valid. I consider it distinct but close to *Peprilus triacanthus*. The relationships and possible interactions of the two species are discussed on p. 247.

Peprilus triacanthus (Peck, 1804)

Figures 21, 22

Stromateus triacanthus Peck, 1804: 48, fig. 2, pl. 2 (original description, Piscataqua River, New Hampshire, holotype not seen); Günther, 1860: 398; Jordan and Gilbert, 1882a: 451; Jordan and Gilbert, 1882b: 597.

Stromateus cryptosus Mitchill, 1814: 3 (original description, New York Bay, holotype not seen); Mitchill, 1815: 365, fig. 2, pl. 1; Cuvier and Valenciennes, 1833: 408.

Rhombus cryptosus, Cuvier and Valenciennes, 1833: 408.

Peprilus triacanthus, Storer, 1839: 60; Haedrich, 1967: 106, fig. 40.

Rhombus triacanthus, DeKay, 1842: 137, fig. 80, pl. 26.

Poronotus triacanthus, Gill, 1861: 35; Jordan and Gilbert, 1878: 377; Bean, 1880: 91; Jordan and Evermann, 1898: 2849, fig. 405, pl. CL (in part IV); Jordan, Evermann, and Clark, 1930: 267; Bigelow and Schroeder, 1953: 363, fig. 192; Briggs, 1958: 292, in part.

Rhombus (*Poronotus*) *triacanthus,* Jordan and Evermann, 1896: 967, *Poronotus* designated as a subgenus.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). ANSP 11350 (1: 95.6 mm, New Hampshire); ANSP 11353 (1:147.8, Maine); FSBC 1024 (2:81.6, 98.2, Atlantic Ocean, Florida, Duval County, jetty at Atlantic Beach, 29 November 1958); MCZ 2375 (1:185.0, Nahant, Massachusetts); MCZ 16722 (1:197.5, Waquoit, Mass.); MCZ 16745 (1:152.5, Nahant, Mass.); MCZ 16815 (2:118.0, 119.0, Malden, Mass.); MCZ 16822 (1:168.5, Provincetown, Mass.); MCZ 16906 (1:67.0, Eastport, Me.); MCZ 16911 (2:116.5, 120.0, Tarrytown, New York); MCZ 16939 (2: 50.0, 72.0, Penikese I., Elizabeth Is., Mass.); *MCZ 17017 (5:94.5–108.0, Hampton Roads, Virginia); MCZ 17173 (1:195.5, Martha's Vineyard, Mass.); MCZ 17175 (1:164.5, Trenton, New Jersey); MCZ 17207, 17208 (2:138.0, 194.5, Waquoit, Mass.); MCZ 17304 (1:166.5, Cape Cod, Mass.); MCZ 23406 (1:179.0, Nahant, Mass.); MCZ 23928 (1:186.0, New York Harbor, N. Y.); MCZ 25768 (16:10.6–24.6, Newport, Rhode Island, 6 CS); MCZ 34601 (3:57.0–68.0, ALBATROSS II 20852, Mass., 58 m, 14 July 1930); MCZ 34602 (2:26.5, 28.3, Nantucket I., Mass., 24 August 1925); MCZ 42122 (4:7.7–29.7, 39°28′N, 71°10′W, to 39°27′N, 71°26′W, 57 m, R/V ATLANTIS RHB 604, IKMT, 22–23 July 1954, CS); MCZ 42123 (1:113.0, Port Royal, South Carolina); *MCZ 43227 (3:144.0–156.0, Assateague I., Maryland, 10 July 1957); *MCZ 44974 (9:60.0–115.0, Georgia, off Jekyll Island, 25 March 1959, 1 CS); MCZ 44977 (1:121.0, 31°06′N, 79°56.5′W, 46–55 m, M/V SILVER BAY Sta. 5709, 8 May 1964); MCZ 45038 (4:76.5–175.0, Ga., commercial trawling area, 19 August 1959); MCZ 45117 (10:94.5–138.6, Point Judith, R. I., June, 1958); MCZ 45126 (2: 110.2, 121.9, North Carolina, 34°45′N, 76°21′W, 16 m, M/V SILVER BAY Sta.

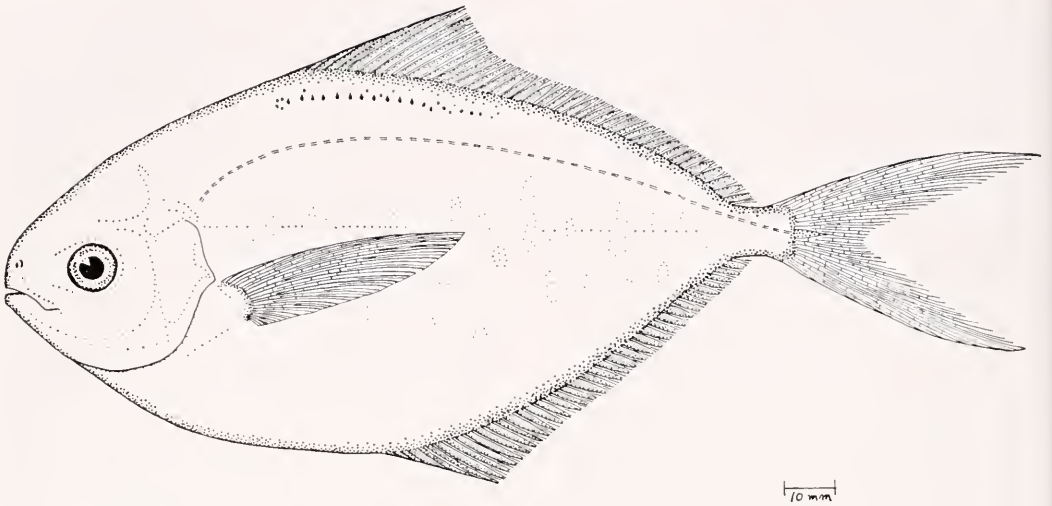


Figure 21. *Peprilus triacanthus*, 157.8 mm SL, fish morket, Cambridge, Massachusetts.

1641, 24 February 1960); MCZ uncat. (11:115.0–183.5, Waquoit, Mass.); MCZ uncat. (15:20.5–40.8, E of Long Island, N. Y., 40°46′N, 70°55′W, 5 m, EUGENIE VIII, Cr. 8, Sta. 1, 19–20 August 1961, plankton net on end of longline, 2 CS); *MCZ uncat. (4:122.5–153.0, E of Long I., N. Y., 40°01′N, 71°23′W, bottom to 128 m, CAP'N BILL III, Cr. 65–1, Bait sta. 1, 5 May 1965); *MCZ uncat. (14:106.0–198.0, N. C., 36°30′N, 74°45′W, 110 m, M/V SILVER BAY Sta. 4104, 31 May 1962, 1 radiographed); *TABL 101984 (13 meas.:55.2–138.8, Atlantic Ocean, 30°31′N, 81°22′W, 13 m, M/V SILVER BAY Sta. 3464, 5 October 1961, 17 radiographed); TABL 101990 (1:23.0, Atlantic Ocean, 30°15′N, 80°59′W, 29 m, M/V SILVER BAY Sta. 2795, 7 February 1961, larval trawl); TABL 101991 (1:21.0, Atlantic Ocean, 27°38′N, 80°02′W, 48–57 m, M/V SILVER BAY Sta. 5559, 8 March 1964, nekton net); TABL 101992 (3:9.6–19.8, Atlantic Ocean, 30°46′N, 80°48′W, 25 m, M/V SILVER BAY Sta. 2804, 9 February 1961, larval trawl); TABL 101993 (1:19.0, Atlantic Ocean, 27°43′N, 80°00.5′W, 57 m, M/V SILVER BAY Sta. 5560, 8 March 1964, 1 m, nekton net); TABL 102050 (1:15.0, Atlantic Ocean, 27°21.5′N, 79°57.5′W, 101 m, M/V SILVER BAY Sta. 5551, 7 March 1964); TABL uncat. (1:132.0, Atlantic Ocean, 29°48′N, 80°12′W, 348–366 m, M/V SILVER BAY Sta. 470, 17 June 1958); TABL uncat. (1:119.5, N. C., 34°17′N, 75°55′W, 183–201 m, M/V OREGON Sta. 4973, 29 July 1964); *USNM 311? (1:122.0, Atlantic Ocean, 29°38′N, 80°09′W, 320–329 m, M/V SILVER BAY Sta. 471, 17 June 1958); USNM 156113 (1:72.0, Cape Kennedy, Florida); *USNM 156149 (6 meas.: 54.0–79.0, Fernandina, Fla., March, 1920, 13 radiographed); *USNM 156153 (5:69.0–76.0, Fernandina, Fla., March, 1918); *USNM 158133 (3:116.0–127.0, Atlantic Ocean, 28°03′N, 79°52′W, 274–320 m, M/V PELICAN Sta. 25, 8 April 1956); *USNM 159807 (1:131.0, Atlantic Ocean, 29°15′N, 80°05′W, 384 m, M/V COMBAT Sta. 329, 31 May 1957); USNM 159813 (2:73.0, 79.0, Atlantic Ocean, 30°24′N, 81°22′W, 11–15 m, M/V COMBAT Sta. 504, 2 October 1957); *USNM 159818 (1: 61.0, Atlantic Ocean, 29°30′N, 80°11′W, 137 m, M/V COMBAT Sta. 489, 19 August 1957); USNM 159823 (1:75.0, Ga., 31° 29′N, 79°33′W, 110 m, M/V COMBAT Sta. 512, 3 October 1957); USNM 188468 (4:

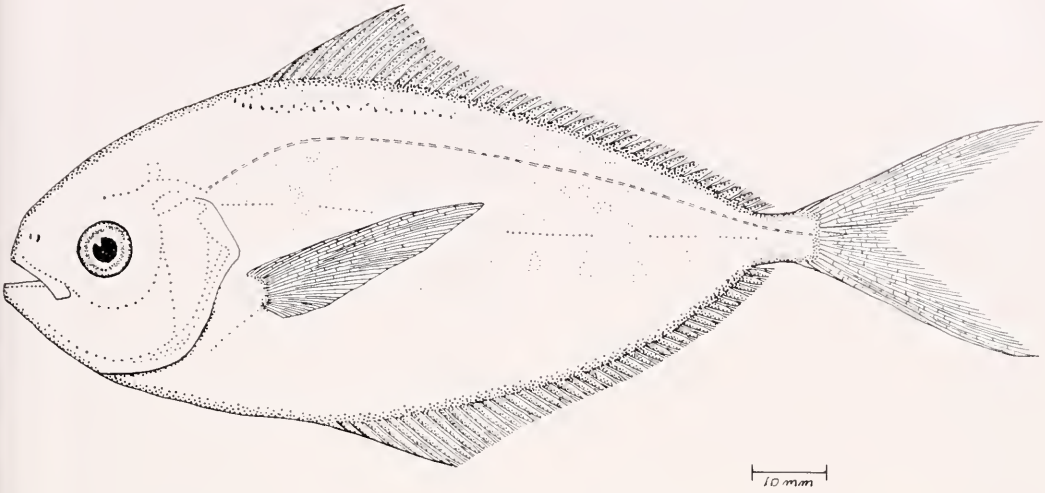


Figure 22. *Peprilus triacanthus*, 122.0 mm SL, off eastern Florida at 320 to 330 m, USNM, SILVER BAY Station 471.

101.0–110.0, Atlantic Ocean 30°39′N, 76° 39′W, 229 m, M/V COMBAT Sta. 180, 16 November 1956); *USNM 190367 (10: 61.0–141.0, N. C., 35°01.5′N, 76°02.5′W, 9–15 m, M/V SILVER BAY Sta. 1487, 7 December 1959, 8 radiographed); USNM uncat. (5:95.0–111.0, Delaware, about 15 miles NE of Indian River Inlet, 16 m, 4–5 August 1958); *USNM uncat. (10:133.0–180.0, Atlantic Ocean, 29°45′N, 80°10′W, 329–348 m, M/V SILVER BAY Sta. 489, 21 June 1958, 8 radiographed); *USNM uncat. (4:108.0–132.0, Atlantic Ocean, 29° 45′N, 80°20′W, 64–68 m, M/V SILVER BAY Sta. 5687, 1 May 1964); UMML 2479 (1:110.5, Atlantic Ocean, 30°02′N, 80° 06′W, 320 m, M/V PELICAN Sta. 49, 12 May 1956); UMML 2924 (1:169.0, Jacksonville, Fla., to Brunswick, Ga., 37–91 m, January, 1956); UMML 4370 (2:105.1, 106.2, N. C., 34°07′N, 76°06′W, 229 m, M/V COMBAT Sta. 175, 15 November 1956); UMML 4497 (1:110.4, Fla., ESE off St. John's River, 1 May 1952); UMML 6937 (2:77.3, 81.7, Atlantic Ocean, St. Augustine, Fla., 7–13 m, 4 August 1960); UMML 7053 (1:111.8, N. C., 34°36′N, 76°13′W, 33–37 m, M/V SILVER BAY Sta. 1643, 24 February 1960); UMML 7340 (10:76.7–98.8, N. C., 34°57′N, 76°03′W, 16–18 m, M/V SILVER BAY Sta. 1631, 23 February 1960); UMML 7614 (1:144.6, S. C., 32°59.5′N, 79°14′W, 9–11 m, M/V SILVER BAY Sta. 1365, 21 October 1959); UMML 8102 (1:64.4, Atlantic Ocean, St. Augustine, Fla., 15–16 m, 29 November 1960); UMML 8527 (1:138.3, Atlantic Ocean, St. Augustine, Fla., 14–15 September 1960); UMML 15049 (1:108.2, Ga., 31°26′N, 79°44′W, 84–102 m, M/V SILVER BAY Sta. 5385, 4 December 1963); UMML 17171 (1:103.0, Ga., 32°01′N, 79° 10′W, 137–146 m, M/V SILVER BAY Sta. 5397, 7 December 1963); *UW 13407 (1: 136.6, Gulf of Mexico, NE of Tortugas Light, 12 February 1954, shrimp trawl).

Diagnosis. *P. triacanthus* is an elongate species with slightly falcate dorsal and anal fins. It is distinguished from *P. paru* by having a more elongate body – mean body depth of 458 compared to 710 for *P. paru*, each in thousandths of SL; a row of relatively large pores below the anterior half of the dorsal fin; and slightly falcate dorsal and anal fins rather than moderately or extremely falcate ones. Characters that distinguish *P. triacanthus* from *P. burti* and *P. simillimus* are listed in the diagnosis

Table 17. Proportional Measurements of *Peprilus triacanthus*. Symbols as in Table 7. Size range, 10.6–198.0 mm SL; mean size, 102.4 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	182	251–358	289	1.87	8.72
Snout length	182	055–090	071	0.57	10.86
Eye diameter	194	061–133	086	1.12	18.15
Length of upper jaw	182	064–113	085	0.69	10.93
Interorbital width	182	072–111	092	0.62	9.09
Length of pectoral fin	177	179–364	312	2.60	11.06
Predorsal distance I	138	332–492	381	3.23	9.98
Predorsal distance II	182	228–407	278	2.82	13.67
Preanal distance	182	375–544	445	2.23	6.76
Maximum depth of body	203	364–600	458	3.28	10.22
Least depth of caudal peduncle	182	055–089	070	0.54	10.36
In thousandths of HL:					
Snout length	182	175–309	252	1.96	10.49
Eye diameter	182	232–377	292	2.41	11.14
Length of upper jaw	182	239–348	295	1.50	6.87
Interorbital width	182	245–389	320	2.26	9.51

Table 18. Meristic Values of *Peprilus triacanthus*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	150	40–48	44.3	0.13	3.63
Anal fin-rays*	152	37–44	40.3	0.11	3.47
Pectoral fin-rays	149	17–22	20.7	0.07	3.96
Total gill rakers	33	22–25	23.8	0.18	4.33
Total vertebrae	279	30–33	31.7	0.03	1.61
Lateral-line scales	9	96–105	–	–	–

* Excluding spines.

of each of these species, respectively. The specific epithet, *triacanthus*, is from the Latin and means "three spines"; it refers to the first dorsal spine, the first anal spine, and the spine on the ventral surface of the pelvic bone, not to the usual presence of three dorsal and three anal spines.

Description. Proportional measurements are given in Table 17 and meristic values in Table 18. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly to moderately convex. Eye diameter greater than length of snout, eye moderately large. Dorsal and anal fins slightly falcate, longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. The system is often very conspicuous in living or freshly collected specimens. An irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. Premaxillary teeth slightly recurved, usually with three small cusps. Swimbladder delicate, thin-walled, elongate, found only in specimens smaller than about 100 mm SL. Dorsal and upper ventral surfaces of the body quite often mottled with large, dark spots; otherwise, coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 6.9 to 18.2 (Table 17) and from 1.6 to 4.3 for meristic characters (Table 18). High V values for proportional measurements indicate considerable variability. Partly it

is due to allometry, especially in eye size, and partly to the inclusion in the sample of members of both the shallow and deep-bodied populations from the southern part of the range. Another source of variability, compared to some of the other species, is the inclusion in the sample of individuals of a broad size-range.

The sample size of *P. triacanthus* used (Table 17) is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). The main exception is vertebral number which, as in all the species of *Peprilus*, is relatively constant (Table 5). Variation in vertebral number is slightly higher in this species than in the others and partly due to differences in the two populations in the southern part of the range.

Geographic variation. Two distinct populations apparently exist off the southeastern coast of the United States, one in deep water generally over a mud bottom, and one in shallower water generally over a sand bottom (Table 22). The deep-water fish (Fig. 22) tend to be more elongate with numerous spots on the body and with 18 or 19, usually 19, caudal vertebrae. Those from shallow water tend to be deeper-bodied with no spots and with 17 to 19, rarely 19, caudal vertebrae (similar to *P. burti*, Fig. 19). The *triacanthus–burti* situation is discussed on p. 247.

No other geographic variation was noted.

Ontogenetic change. Few and moderate changes accompany growth in *P. triacanthus* in a size range of about 10 to 198 mm SL. As shown by ratio-on-size diagrams (Fig. 23), head length, eye diameter, and body depth decrease in size relative to SL with growth while the relative length of the pectoral fin increases up to about 100 mm SL, then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient of the size-on-size regression of eye diameter is relatively low (Fig. 3; Table 6).

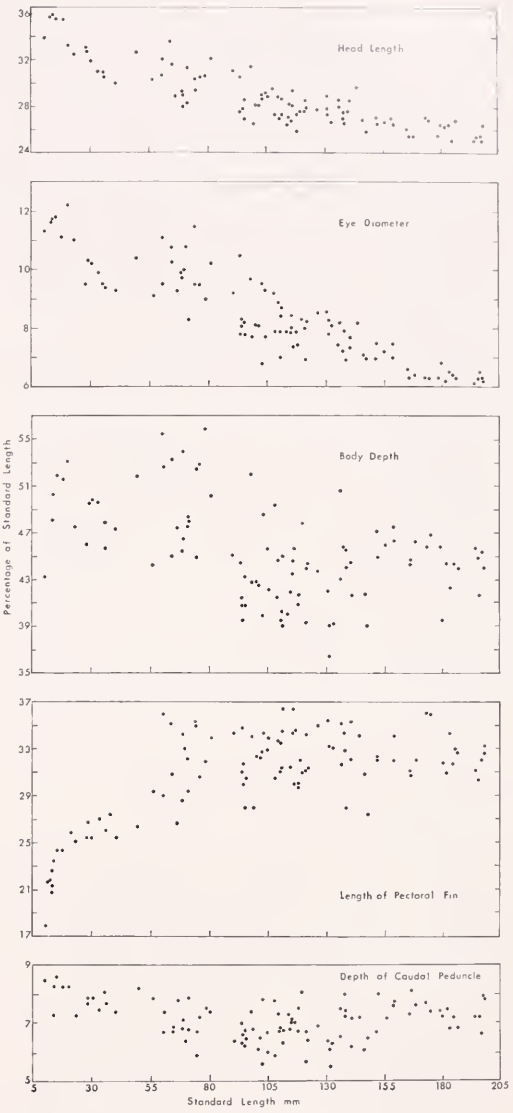


Figure 23. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus triacanthus*.

Distribution (Fig. 7). *P. triacanthus* is known from off the Atlantic Coast of North America from about 48°N in the Gulf of St. Lawrence to about 27°30′N off southern Florida. The species is infrequently collected as far north as the south and east

coasts of Newfoundland (Bigelow and Schroeder, 1953), Cape Breton Island (Hoar, 1937), and the outer coast of Nova Scotia (McKenzie, 1939). It occurs in the Gulf of Maine in the summer and autumn. Southward, the species ranges to southern Florida in shallow water (for example, 27°28′N, 80°02′W, 35 m, M/V OREGON Sta. 5319) and to a similar region in deeper water (for example, 28°03′N, 80°29′W, 274–320 m, M/V PELICAN Sta. 25). I have identified one specimen of *P. triacanthus* from the Gulf of Mexico, a male, 136.6 mm SL, from "NE of Tortugas Light" (UW 13407).

Taxonomic comments. Until Haedrich's (1967) revision of the suborder Stromateoidei, the species had been known almost exclusively as *Poronotus triacanthus*. The chief basis for the generic distinction was the presence of a row of relatively large pores below the dorsal fin, a character more reasonably considered as a specific one. For other relevant taxonomic comments, see under *P. burti*.

Peprilus paru (Linnaeus, 1758)

Figures 24, 29

Stromateus paru Linnaeus, 1758: 248 (based on Sloane's (1725) description, Old Harbour, Jamaica, holotype not seen); Jordan and Gilbert, 1882a: 914; Jordan and Gilbert, 1882b: 596; Fordice, 1884: 312.

Chaetodon alepidotus Linnaeus, 1766: 460 (original description, Charleston, South Carolina, holotype not seen).

Rhombus alepidotus, Lacépède, 1800: 321.

Sternoptyx gardenii Bloch and Schneider, 1801: 494 (original description, Carolina, holotype not seen (after Linnaeus)).

Stromateus longipinnis Mitchill, 1815: 366 (original description, New York Bay, holotype not seen).

Seserinus xanthurus Quoy and Gaimard, 1824 (original description, Rio de Janeiro, Brazil, holotype not seen); Fowler, 1906: 119.

Peprilus crenulatus Cuvier, 1829: 214 (original description, locality ?, holotype not seen); Cuvier, 1836–1849: 141, fig. 3, pl. 64.

Rhombus longipinnis, Cuvier and Valenciennes, 1833: 401, pl. 274; DeKay, 1842: 136, fig. 239, pl. 74.

Rhombus argentipinnis Cuvier and Valenciennes, 1833: 405 (original description, Montevideo, Uruguay, holotype not seen).

Rhombus xanthurus, Cuvier and Valenciennes, 1833: 405; Jordan and Evermann, 1898: 2849.

Rhombus crenulatus, Cuvier and Valenciennes, 1833: 410, pl. 275.

Peprilus longipinnis, Cuvier, 1836–1849, fig. 2, pl. 63 (in Atlas by Valenciennes); Gill, 1861: 35.

Stromateus gardenii, Günther, 1860: 399.

Rhombus orbicularis Guichenot, 1866: 245 (original description, Cayenne, French Guiana, holotype not seen).

Peprilus alepidotus, Goode, 1879: 112; Goode and Bean, 1879: 130; Bean, 1880: 92; Bigelow and Schroeder, 1953: 368; Briggs, 1958: 292; Springer, 1961: 482; Haedrich, 1967: 106, fig. 41.

Stromateus alepidotus, Jordan and Gilbert, 1882a: 451; Jordan, 1884: 149; Bean and Dresel, 1884: 156.

Rhombus (*Rhombus*) *paru*, Jordan and Evermann, 1896: 965, *Rhombus* a genus and a subgenus.

Rhombus (*Rhombus*) *xanthurus*, Jordan and Evermann, 1896: 966, *Rhombus* a genus and a subgenus.

Rhombus paru, Jordan and Evermann, 1898: 2849, fig. 404, pl. CL (in Part IV).

Peprilus paru, Evermann and Marsh, 1900: 141, fig. 39; Meek and S. F. Hildebrand, 1925: 411; Jordan, Evermann, and Clark, 1930: 266; Briggs, 1958: 292; Haedrich, 1967: 106.

Seserinus paru, Fowler, 1916: 402; Fowler, 1942: 152.

Sesserinus xanthurus, Fowler, 1942: 152 (error in spelling of generic name; referable to *Seserinus xanthurus* Quoy and Gaimard, 1824).

Simobrama xanthura, Fowler, 1944: 3, fig. 2.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). FSBC 306 (1:63.6 mm, Gulf of Mexico, Florida Keys, 24°41′–52′N, 82°00′–35′W, 14–15 January 1958); FSBC 1745 (2:90.9, 95.5, Gulf of Mex., Fla., Pinellas Co., Johns Pass, Madeira Pass, 25 April 1960); FSBC 2282 (4:75.1–83.8, Mississippi, Horn I., 27 October 1962); FSBC 2572 (1:71.0, Gulf of Mex., Fla., 27°43′N, 82°45′W, 24 February 1963); FSBC 2562 (6:65.6–95.9, Gulf of Mex., Fla., 27°43′N, 82°45′W, 19 Decem-

ber 1962); FSBC 3831 (2:92.0, 138.0, Gulf of Mex., Fla., Tampa Bay, 1 mile S of MacDill AFB, 23 January 1966); FSBC 3956 (3:74.0–149.0, Gulf of Mex., Fla., Pinellas Co., 27 December 1966); IMS 325 (1:63.0, near Pass Cavallo, Texas, 6–11 m, 22 October 1960); IMS 326 (1:106.7, Tex., 18 miles W of Sabine, 12 m, 15 June 1951); IMS 333 (2:42.5, 54.0, Tex., Mustang I., 6–7 m, 21 October 1950); IMS 1019 (1: 68.3, near Port Aransas, Tex., 10 July 1962); IMS 1178 (1:137.0, 50 miles E of Port Aransas, Tex., 57–58 m, 6 December 1961); IMS uncat. (9:21.2–61.2, near Port Aransas, Tex., spring, 1964); LACM 4489 (2:61.5, 69.3, Mayagüez, Puerto Rico, October, 1963, 1 CS); *LACM 4988 (1:175.0, Mayagüez, P. R., March, 1964, beach seine); *LACM 4989 (1:172.0, Mayagüez, P. R., March, 1964, beach seine); *LACM 5725 (1:103.7, Jamaica, Kingston market); *LACM 6741–21 (1:70.0, Mayagüez, P. R., 3 December 1966); *LACM 7884 (1:103.3, Mayagüez, P. R., 9 February 1963); MCZ 1687 (1:75.0, Beaufort, North Carolina); MCZ 4600 (1:118.0, Brazil); MCZ 16778 (1:106.0, Brazil); MCZ 16999 (1:73.0, Fla.); MCZ 17104 (2:123.0, 141.0, Rio de Janeiro, Brazil); MCZ 17129 (2:132.0, 137.0, Pensacola, Fla.); MCZ 17336 (1: 123.0, Fla. Keys); MCZ 17364 (1:131.0, Penikese I., Elizabeth Is., Mass.); MCZ 26291 (1:106.0, Mobile, Alabama); MCZ 41064 (2:47.4, 56.3, Port au Prince, Haiti, August, 1950); *MCZ uncat. (5:112.0–148.5, Port Aransas, Tex., 6–7 m, 3 July 1967, tide trap, 2 radiographed); MCZ uncat. (1:60.0, N. C., Bogue Sound, August, 1966, CS); *SU 2774 (3:124.3–140.0, Washington market); *SU 4900 (2:136.9, 168.6, Jamaica); *SU 14025 (1:222.0, Argentina, Buenos Aires market, 1934); *SU 38704 (3:76.5–80.6, Aransas Pass, Tex., 12 May 1940); *SU 51811 (2:98.7, 105.5, Recife, Brazil, 23 November 1944); *TABL 101976 (1:137.8, Honduras, off Caratasca Lagoon, 15°49.5′N, 83°44′W, 31 m, R/V UNDAUNTED Cr. 6703, 7 April 1967); *TABL 101977 (7:115.7–130.1, Honduras, off Caratasca Lagoon, 15°54′N, 83°40′W, 37 m, R/V UNDAUNTED Cr. 6703, 8 April 1967); *TABL 101978 (2:85.4, 103.6, Honduras, off Caratasca Lagoon, 15°45′N, 83° 32′W, 33–37 m, R/V UNDAUNTED Cr. 6703, 9 April 1967); *TABL 101979 (1: 132.4, Honduras, off Caratasca Lagoon, 15°56′N, 83°41′W, 37–40 m, R/V UNDAUNTED Cr. 6703, 12 April 1967); *TABL 101980 (2:102.9, 107.5, Honduras, off Caratasca Lagoon, 15°19′N, 83°26′W, 9 m, R/V UNDAUNTED Cr. 6703, 10 April 1967); *TABL 101982 (3:84.8–96.5, Honduras, off Caratasca Lagoon, 15°21′N, 83°34′W, 9 m, R/V UNDAUNTED Cr. 6703, 10 April 1967); *TABL 101983 (2: 114.8, 123.0, British Honduras, Belize, 17° 12′N, 88°11.2′W, 18–20 m, R/V UNDAUNTED Cr. 6703, Sta. 72, 18 May 1967); *TABL uncat. (2:106.2, 134.9, Guyana, about 8°45′N, 59°15′W, 29 m, M/V CALAMAR Sta. 72, 18 June 1967); *TABL uncat. (7:82.2–97.7, Guyana, about 7°N, 58°30′W, near mouth of Essequibo River, M/V CALAMAR Sta. 82, 20 June 1967); *TABL uncat. (6:56.4–121.2, Surinam, about 6°N, 55°30′W, 20 m, M/V CALAMAR Sta. 102, 15 July 1967); *TABL uncat. (1:88.1, Surinam, about 6°N, 54°30′W, 20 m, M/V CALAMAR Sta. 100, 14 July 1967); *TABL uncat. (1:104.2, Surinam, about 6°N, 54°30′W, 27–29 m, M/V CALAMAR Sta. 121, 11 August 1967); *TABL uncat. (2:113.9, 154.2 Surinam, about 6°N, 54° 30′W, 22–24 m, M/V CALAMAR Sta. 84, 21 June 1957); *TABL uncat. (3:78.5–90.4, Surinam, about 6°N, 54°30′W, 16–18 m, M/V CALAMAR Sta. 133, 15 August 1967); TABL uncat. (1:45.6, Georgia, Jekyll I. beach, 19 July 1956); TABL uncat. (1:62.6, Ga., commercial trawling area, 16 January 1957); TABL uncat. (1:100.2, Ga., commercial trawling area, 6 July 1959); TABL uncat. (2:80.6, 115.4, Ga., commercial trawling area, 12–18 July 1959); TABL uncat. (4: 50.7–108.0, Ga., commercial trawling area, 26–30 July 1959); TABL uncat. (3:61.3–85.7, Ga., commercial trawling area, 6 August 1959); TABL uncat. (1:177.0,

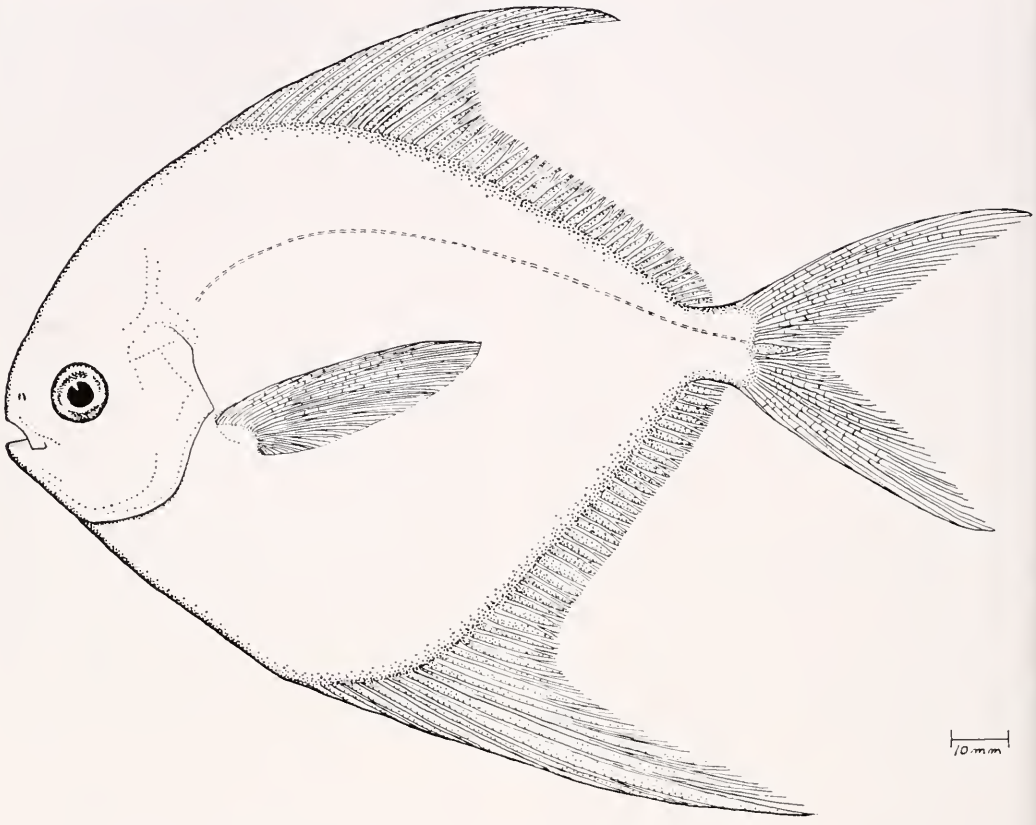


Figure 24. *Peprilus paru*, 126.8 mm SL, Port Aransas, Texas, MCZ uncatalogued.

Trinidad, Port of Spain market, M/V OREGON, 26 September 1964); TABL uncat. (2:146.0, 172.0, Venezuela, 9°32′N, 60°24′W, 60 m, M/V OREGON Sta. 2348, 20 September 1958); TABL uncat. (2: 140.0, 146.0, off Campeche, Mexico, 20° 01′N, 91°47′W, 55 m, M/V SILVER BAY Sta. 844, 17 November 1958); TABL uncat. (1:68.4, N. C., 33°57.5′N, 77°50.5′W, 11 m, M/V SILVER BAY Sta. 1666, 27 February 1960); TABL uncat. (5:67.4–76.3, South Carolina, 32°55.5′N, 79°29′W, 9 m, M/V SILVER BAY Sta. 5423, 11 January 1964); TABL uncat. (1:135.8, Atlantic Ocean, Fla., 28°04′N, 80°11.5′W, 27–29 m, M/V SILVER BAY Sta. 5513, 29 February 1964); *TU 4396 (10:57.6–101.5, Louisiana, Terrebonne Co., mouth of Oyster Bayou, 31 October 1952); TU 9224 (10:25.5–33.1, La., Lake Pontchartrain, 2 miles SE of south draw, 30°10′N, 89°55′W, 11 August 1954); *USNM 3083 (3:50.0–63.0, Plum Point, Maryland, 22 August 1949); *USNM 30064 (1:153.0, Jamaica); *USNM 63660 (1:147.0, P. R., San Juan market); *USNM 63655 (1:114.0, Tex., Matagorda Bay); *USNM 83362 (2:93.0, 94.0, Rio de Janeiro, Brazil); *USNM 86716 (1:131.0, Uruguay); *USNM 117650 (1:152.0, Paraguay ?); *USNM 118637 (6:118.0–140.0, Galveston, Tex., 2 June 1940, 4 radiographed); *USNM 123044 (3:66.0–68.0, Golfo de Venezuela, Piedras Bay, 14 March 1925, USS NIAGARA); *USNM 156134 (8:55.0–93.0, Aransas Pass, Tex., GRAMPUS Sta. 10476); *USNM 158505 (10:115.0–155.0,

Tex., E of Padre I., 27°32.5′N, 96°28′W, 60 m, M/V OREGON Sta. 4, 25 May 1950); UMML 187 (1:155.0, Belize, British Honduras, 17°10′N, 88°18′W, 27 September 1956); UMML 2085 (1:87.7, Dry Tortugas, 24°45′–50′N, 82°10′–30′W, 1955–1956); UMML 8271 (1:57.3, Atlantic Ocean, St. Augustine, Fla., 21 December 1960); UMML 12422 (1:93.0, French Guiana, 5°48′N, 52°53′W, 44 m, M/V OREGON Sta. 4190, 22 February 1963); UMML 13462 (1:60.8, Atlantic Ocean, St. Augustine, Fla., 1 February 1961); UMML 13986 (1:86.5, Surinam, 6°16′N, 55°56′W, 27 m, M/V OREGON Sta. 4171, 19 February 1963); UMML 16374 (1:49.2, Gulf of Mex., Fla., Okaloosa Co., 9–10 September 1963); UMML 16817 (2:18.2, 25.7, Fla., Monroe Co., Everglades Natl. Park, Shark River Delta, 5 November 1964); UMML 17068 (1:142.5, Colombia, 9°35′N, 76°04.5′W, 40–55 m, M/V OREGON Sta. 4895, 26 May 1964); UMML 21799 (2:99.5, 102.4, Golfo de Venezuela, 11°46′N, 71°16′W, 24 m, M/V OREGON Sta. 5670, 6 October 1965); UMML 21812 (2:30.3, 50.1, Golfo de Venezuela, 11°27′N, 71°39′W, 27 m, M/V OREGON Sta. 5673, 6 October 1965); UMML 22232 (1:110.0, Colombia, 8°48′–46.8′N, 76°39.7′–42.8′W, R/V PILLSBURY Sta. 360, 12 July 1966); WHOI 66264B (1:83.0, Carmen, Mex., about 18°N, 92°W, 15 March 1950).

Diagnosis. *P. paru* is a very deep-bodied species with moderately to extremely falcate dorsal and anal fins. The longest rays of each fin are six or more times the length of the shortest rays of each fin. Characters that distinguish *P. paru* from *P. burti*, *P. triacanthus*, and the related *P. medius* are listed in the diagnosis of each of these species, respectively. The specific epithet, *paru*, is a Brazilian name used by Linnaeus (1758) following Sloane's (1725) designation of the species as "Paru pisci Brasiliensi Congener."

Description. Proportional measurements are given in Table 19 and meristic values in Table 20. Body ovate, very deep, compressed; anterior dorsal profile moderately to strongly convex. Eye diameter greater than length of snout; eye relatively large. Dorsal and anal fins moderately to extremely falcate, longest dorsal and anal rays six or more times the length of shortest dorsal and anal rays; anterior anal rays often extremely long, as much as 20 to 25 times the length of shortest ray. Dorsal fin with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin slightly shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape; pores very small on body and usually not visible except in small individuals. Premaxillary teeth slightly recurved, pointed, simple. Swimbladder delicate, thin-walled, elongate; found only in specimens smaller than about 100 mm SL. Coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 5.8 to 14.5 (Table 19) and from 0.6 to 5.1 for meristic characters (Table 20). Relatively high V values indicate considerable variability and are partly due to: allometry, especially in eye size; the inclusion of a wide size-range of individuals in the sample; and, to irregular variation over the broad geographic range of the species.

Meristic characters other than vertebral number and gill raker number vary more than in the other species of the genus (Tables 1 to 5). Dorsal, anal, and pectoral fin-ray numbers vary geographically and are discussed below.

Geographic variation. *P. paru* occurs along the Atlantic Coast of the United States from Chesapeake Bay or just northward to Florida, in the Gulf of Mexico, in the West Indies, along the coast of Central

Table 19. Proportional Measurements of *Peprilus paru*. Symbols as in Table 7. Size range, 18.2–222.0 mm SL; mean size, 94.3 mm SL.

	N	R	$\bar{x}$	SE	V
In thousandths of SL:					
Head length	182	251–396	305	1.93	8.54
Snout length	195	044–084	062	0.56	12.63
Eye diameter	202	058–147	103	1.05	14.46
Length of upper jaw	182	065–112	084	0.68	10.90
Interorbital width	182	085–144	112	0.84	10.14
Length of pectoral fin	196	274–454	386	2.51	9.11
Predorsal distance I	182	369–503	435	2.12	6.57
Predorsal distance II	179	258–399	319	2.02	8.48
Preanal distance	182	369–636	484	3.27	9.13
Maximum depth of body	205	565–877	710	4.25	8.57
Least depth of caudal peduncle	191	066–112	092	0.58	8.66
In thousandths of HL:					
Snout length	182	148–247	204	1.41	9.35
Eye diameter	182	228–442	334	2.35	9.51
Length of upper jaw	182	233–318	275	1.19	5.82
Interorbital width	182	245–479	368	1.74	6.37

Table 20. Meristic Values of *Peprilus paru*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	178	38–47	42.9	0.12	3.75
Anal fin-rays*	176	35–45	40.4	0.14	4.73
Pectoral fin-rays	172	18–24	21.9	0.09	5.11
Total gill rakers	98	20–23	21.5	0.07	3.12
Total vertebrae	182	29–31	30.0	0.01	0.57
Lateral-line scale	22	80–95	–	–	–

* Excluding spines.

America, and along the coast of South America, rather abundantly to Rio de Janeiro, and less commonly to Argentina. After the publication of "The Marine Fishes of Panama" by Meek and S. F. Hildebrand (1925), Hildebrand (MS) stated that there were two distinct species among the populations of *P. paru:* 1) *P. alepidotus* from the Atlantic Coast of the United States and the Gulf of Mexico; and 2) *P. paru* from the West Indies, Central America, and South America. He noted that *P. paru* differed from *P. alepidotus* in having a more robust body, larger scales, and slightly shorter (fewer rays) dorsal and anal fins, particularly the anal. Hildebrand also stated that while each has an equal number of pectoral rays, *P. paru* has a narrower pectoral and a less falcate dorsal fin than *P. alepidotus.* His findings were based on numerous specimens from the United States, two from the West Indies, two from Panama, five from Venezuela, four from Brazil, and five from Uruguay.

Following Hildebrand's analysis, *P. paru* and *P. alepidotus* have been considered distinct in faunal and fishery works.

Based upon the examination of 207 specimens from throughout the species range, I find only partial agreement with Hildebrand's conclusions. Although body proportions do vary, I could not detect geographic variation of characters reflecting the "robustness" of the body, nor could I find decided differences in the size of the scales or in the shape of the pectoral fin. Some slight differences may exist in the above three characters but do not seem of sufficient magnitude to warrant distinction. Contrary to Hildebrand's statement that the dorsal fin of *P. alepidotus* is more falcate than that of *P. paru,* I find that the length of the anterior lobes of both dorsal and anal fins tends to increase in a north-to-south direction. This follows a general trend existent in a number of fish groups – that the fins are longer in more

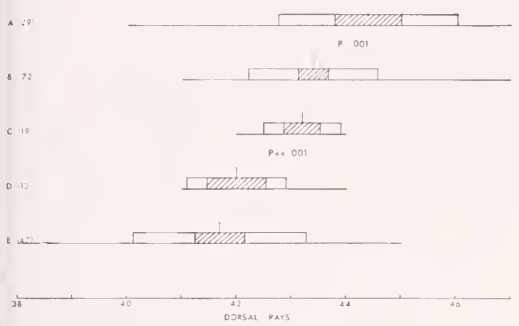


Figure 25. Geographic variation in the number of dorsal fin-rays of *Peprilus paru*: A = United States, Atlantic Ocean; B = Gulf of Mexico; C = Central America; D = West Indies; E = South America; numbers in parentheses are sample sizes. The horizontal line represents the range of values; the vertical line represents the mean; the large, hollow rectangle represents one standard deviation on either side of the mean; the small, barred rectangle represents the 95 per cent confidence interval. Each P value is for comparison of the two sample means immediately above and below the value; only P values of 2 per cent or less are listed.

tropical waters (Frederick H. Berry, personal communication). In *P. paru* it appears to be partly an individual variation since certain fish from a single sample may have extremely falcate dorsal and anal fins.

The counts of the dorsal, anal, and pectoral rays vary geographically, but in each case the variation is clinal rather than being a basis for dividing the populations into two distinct species. The clines are in an irregular north-to-south pattern and are diagrammed in Figures 25 to 27 in a manner generally following the method of Hubbs and Hubbs (1953).

The number of dorsal rays shows a regular gradient in the manner in which I have arranged the regions (Fig. 25) although, in a strictly latitudinal sense, the positions of the West Indies and Central America should probably be reversed. The ranges of values overlap widely, but in proceeding from one coastal region to another in a north-to-south direction, the sample from the United States Atlantic shows a significant difference from the

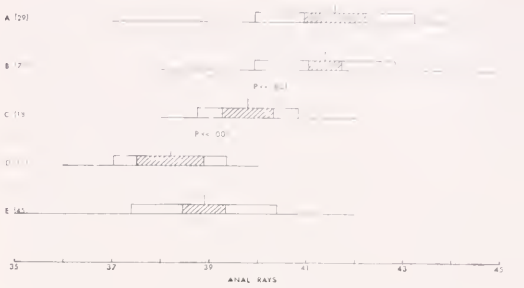


Figure 26. Geographic variation in the number of anal fin-rays of *Peprilus paru*. Explanation of symbols in Figure 25.

Gulf of Mexico sample, and the Central American population has a significantly different number from the West Indian and the South American populations. The levels of significance were set at the 2 per cent level using a two-tailed Student's *t*-test.

The greatest difference among populations of the five regions occurs in the number of anal fin-rays, although the ranges of values overlap considerably (Fig. 26). In this character the United States Atlantic and Gulf of Mexico populations are very similar. The latter sample differs significantly from the Central American sample and in turn the Central American one is

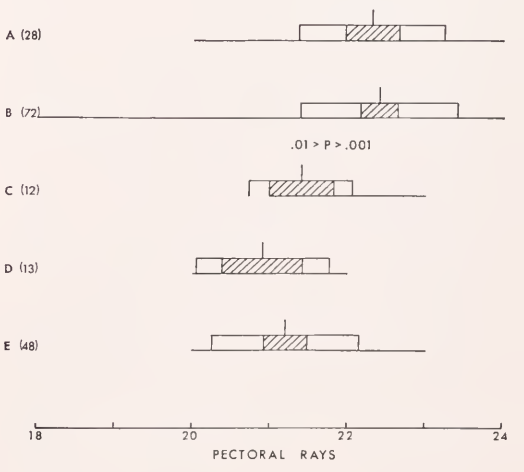


Figure 27. Geographic variation in the number of pectoral fin-rays of *Peprilus paru*. Explanation of symbols in Figure 25.

significantly different at the 2 per cent level from the West Indian sample. The Central American sample is different from the South American one, but only significant at the 2 to 5 per cent level. The West Indian members are the most aberrant among the five regions; however, the sample size (13) is the smallest. The differences in this character among the regional populations do not seem strong enough to suggest a subspecific designation, especially since other characters vary in a different manner.

In the pectoral ray number the gradient is slight, the overlap is considerable, and there is less difference among the populations than in the above two meristic characters (Fig. 27). The Central American population is significantly different from the Gulf of Mexico member, but the southern populations are completely contained in the ranges of values of the United States Atlantic and Gulf populations.

Further evidence for divergence among the populations of *P. paru* has come from an examination of the parasitic isopods which inhabit the gill chambers of this species. Thomas E. Bowman (personal communication) has found that the cymothoid isopods taken from United States Atlantic and Gulf populations are different from those taken from *P. paru* collected off Surinam. The species in the former regions is *Lironeca ovalis* Say (possibly a synonym of *L. redmanni* Leach), while those from the Surinam specimens are very similar in some ways but in other characters are different enough to possibly be considered as members of a distinct species. Specimens from the intermediate areas, West Indies and Central America, are needed to clarify the status of the populations. It may be that the isopods are geographically varying in a manner parallel to their hosts. If there are two species of isopods involved, this would lend support to the recognition of two separate species among the populations of *P. paru*. It would not be conclusive evidence since it is to be expected that rates of differentiation and speciation would be different in the two animal groups.

In summary, there is apparently semi-isolation and some differentiation among regional populations of *P. paru*. Although there is probably no complete break in gene flow, it does appear to be reduced, the reduction effected by barriers of deep water and unfavorable coastlines. *P. paru* is essentially a shallow-water species and would cross deep water only infrequently, probably most commonly by passive transport of eggs and larvae. The species is most abundant in areas where the continental shelf is broad and with large expanses of shallow water. Zones where the shelf is narrow or where the shore is rocky may serve as partial barriers to *P. paru*. Although the distribution of *P. paru* is continuous around Florida, it is uncommon in southern Florida; and there is evidence of slight differentiation between Atlantic and Gulf populations (Fig. 25). Atlantic and Gulf populations differ more significantly in the three meristic characters discussed above from West Indian forms than from the Central American ones. This disparity may be partly due to the gap of deep water separating the United States from the West Indies as compared to continuous coastline from the Gulf to Central America. Some differentiation is apparent between Gulf and Central American populations and may be effected somewhat by the lack of favorable coastlines between the two regions. The West Indian form appears to be most similar to South American members of the species. Continuity and genetic interchange are probably being maintained between these two regions via the shallow coastal areas associated with the chain of West Indian islands. Deep water and unfavorable coastlines are apparently serving to partially isolate Central American populations from the West Indian and South American populations, respectively.

Mayr (1963: 361) states that clines are the product of two conflicting forces:

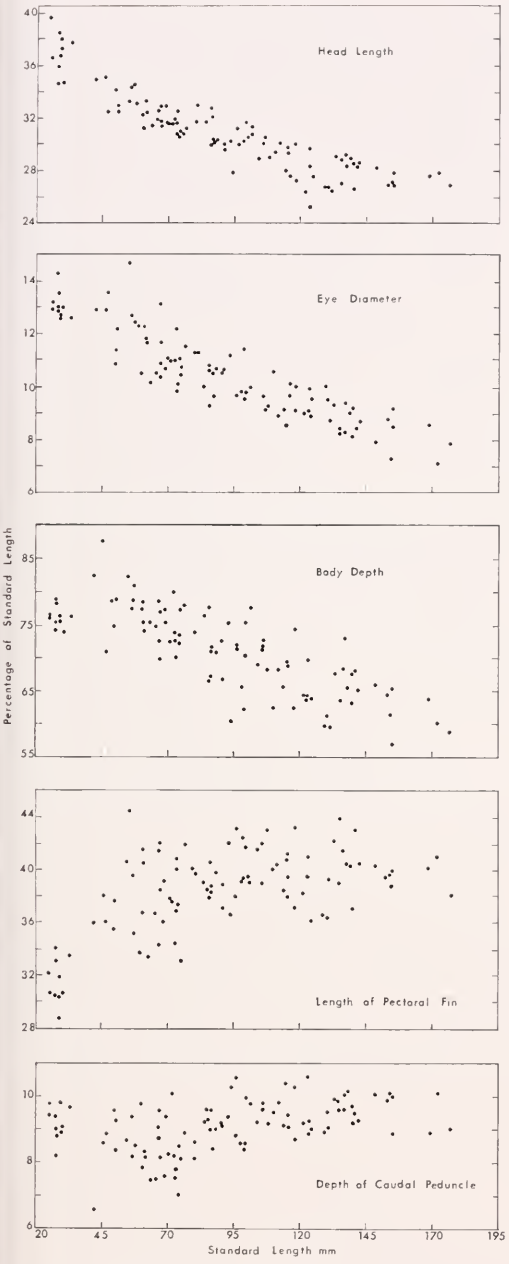


Figure 28. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus paru*.

selection, which would make every population uniquely adapted to its local environment; and, gene flow, which would tend to make all populations of a species identical. Mayr (1963: 365) further states that in many cases gene flow seems responsible for the maintenance of clines to a greater degree than environmental gradients. The cohesive effect of gene flow seems to be exceedingly potent. Although a temperature gradient is probably partially responsible for the clines in characters of *P. paru*, it seems that gene flow between contiguous populations is of equal or greater importance. If temperature were of prime importance, an increase in meristic values in the extreme southern portion of the species range might be expected. I have not found such a pattern.

Ontogenetic change. Few and moderate changes accompany growth in *P. paru* in a size range of about 25 to 177 mm SL. As shown by ratio-on-size diagrams (Fig. 28), head length, eye diameter, and body depth decrease in size relative to SL with growth, while the relative length of the pectoral fin increases up to about 100 mm SL then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient in a size-on-size regression for eye diameter is relatively low (Fig. 3; Table 6).

Distribution (Fig. 7). *P. paru* is known from Chesapeake Bay or just north on the Atlantic Coast of the United States southward around peninsular Florida to throughout the Gulf of Mexico, Central America, and at least part of the West Indies to South America where it commonly occurs to about 23°S in the vicinity of Rio de Janeiro, Brazil, and less abundantly as far south as Argentina. The species infrequently ranges as far north as Long Island and rarely as far as the Gulf of Maine, the most northerly capture being at Cape Elizabeth, Maine, about 43°N (Bigelow and Schroeder, 1953). *P. paru* has been collected near a number of West Indian Islands including Jamaica, Puerto Rico, Haiti, and Trinidad.

Taxonomic comments. Since the descriptions by Linnaeus of *Stromateus paru* in 1758 and *Chaetodon alepidotus* in 1766,

the taxonomic status of the species has been in question. Various names have been applied to this widely-distributed and variable species; hence, the synonymic list is an extensive one.

It has become customary in faunal and fishery works to list *P. alepidotus* as the species along the Atlantic and Gulf coasts of the United States and *P. paru* as the species along the West Indies, Central and South America. *P. paru* is the name sometimes given to the Gulf of Mexico populations, and *P. alepidotus* to the population off the Atlantic Coast of the United States. Briggs (1958) lists both as occurring off the Atlantic and Gulf coasts of the United States; this seems to be the least likely situation. In this study, all populations are included within *P. paru*.

Lütken (1880) listed a fish he called *Stromateus paru* as occurring at the southern end of the Strait of Malacca between Malaya and Sumatra in southeast Asia. His drawing was of a small fish which had pelvic fins. *P. paru* is restricted to the New World and has no pelvic fins. Therefore, this species is excluded from being the fish of Lütken's description. Lütken's drawing may be referable to *Parastromateus* (= *Apolectus*) *niger*, a fish representing a monotypic family of uncertain affinity.

P. paru is commonly known as the "harvestfish." Names less frequently used are "starfish" and "poppyfish."

ASPECTS OF FUNCTIONAL MORPHOLOGY

Information on the morphology and ecology of the members of the genus *Peprilus* is sufficient to allow some interpretations of functional morphology, and differences among the species are great enough to allow consideration of some trends and specializations which appear to be developing. It is instructive to see whether certain trends correspond to those thought to be occurring generally in perciform fishes.

Skeletal features. Ossification of various parts of the skeleton of *Peprilus* appears to occur differentially. Study of cleared-and-stained material of two species, *P. triacanthus* and *P. burti*, shows that the vertebral column is ossified very early. Specimens of 6 or 7 mm SL have the anterior two-thirds of the column almost completely ossified, while the posterior one-third and the hypural plate are in the early stages of ossification. In these same specimens the bones of the head are incompletely ossified; the pectoral girdle is apparently relatively well ossified and the pectoral fin is short and fanlike; the jaw teeth and the teeth of the pharyngeal sac have formed; and the dorsal and anal fins are almost completely absent at this stage. In specimens of 8 to 10 mm SL the epural elements remain unossified while the hypurals are more completely ossified; the median fins, particularly anteriorly, are beginning to ossify. In specimens of 12 to 18 mm SL the rays of the median fins are visible and all parts except the epurals are near complete ossification (stromateids do not have strongly ossified skeletons). The caudal skeleton has by this size range achieved a higher degree of symmetry with the hypural plate occupying a more equal position dorsally and ventrally, and with the urostyle becoming more slender; the epurals have reached almost complete ossification and the caudal fin has begun to fork. In the smallest specimens examined (5 mm SL) the hypural plate had the same degree of fusion as in the adult skeleton – two epural and four hypural elements. At a size range of 25 to 30 mm SL the epurals are ossified and the pectoral fin has become more elongate. No differences in pattern of ossification between the two species were found.

The pattern of ossification may correlate with the behavior of the young fish. Spawning occurs offshore generally, and the young are in the pelagic surface layers of the ocean. After hatching, and until several days after the yolk sac is absorbed,

the larvae are essentially planktonic with probably little locomotor effort of their own. Early vertebral ossification results in a supporting element of some rigidity. Also, the pectoral fins appear early at about four or five days in *P. triacanthus* (Colton and Honey, 1963). As the caudal apparatus and the median fins strengthen through ossification, and as the caudal fin becomes forked, the young fish becomes more independent in locomotion and at a size of 10 to 15 mm SL probably becomes more nektonic than planktonic. The juvenile fish frequently become associated with coelenterate medusae or siphonophores at a size of 10 to 30 mm SL.

Fishes of the genus *Peprilus* and the family Stromateidae in general have deep, compressed bodies, which are deepest in the region of and just posterior to the body cavity. All seven species of *Peprilus* are similar osteologically, and one of the most conspicuous skeletal regions is that surrounding the body cavity and supporting the viscera. This "visceral basket" gives obvious support and protection to the viscera and abdomen. It is formed anteriorly and ventrally by the cleithrum and the large, posteroventrally directed pelvic bones which unite posteriorly to form a single structure. The vertebrae and pleural ribs house the body cavity dorsally. Posteriorly, the enlarged first interhaemal swings posteriorly to meet the haemal spine of the first caudal vertebrae. The pair of elongate postcleithra provide lateral support. An increased number of anal finrays in the stromateids has apparently resulted in the angular position of the first interhaemal.

While most meristic characters of species of *Peprilus* vary considerably, the vertebral number varies only slightly (Table 5). No geographic variation in vertebral number was detected in any of the species, with the possible exception of the complex *burti-triacanthus* situation off the Atlantic coast of the southeastern United States. Variation is so slight that the vertebral count becomes an important specific character in this genus. For the seven species, 1255 vertebral counts were made. Coefficients of variation (Tables 8, 10, 12, 14, 16, 18, and 20) are very low for this character, indicating great homogeneity within a species.

Several authors (Hubbs, 1926; Vladykov, 1934; Tåning, 1952; Bailey and Gosline, 1955; and others) have shown that meristic elements, including vertebrae, are influenced by temperature and that the number of such elements is progressively greater to the north, or at higher altitudes, or in locally colder areas of spawning. Variation in vertebral number in certain fish groups is often so great that the character must be used only with caution, as has been shown by Bailey and Gosline (1955) for darters of the family Percidae. But in *Peprilus* variation is slight and vertebral number is an important distinguishing character. The caudal vertebrae of *Peprilus* vary more than the precaudal ones, a situation found to be a somewhat general one by C. L. Hubbs (1922). It may be that precaudal vertebrae are fixed earlier in development than most other meristic characters, as is true in the paradise fish, *Macropodus opercularis* (Lindsey, 1954).

Constancy of vertebral number may be correlated with certain other characters involved in evolutionary trends. Bailey and Gosline (1955) have stated that in the family Percidae decreased size is apparently, and probably casually, correlated with reduction in vertebral number. Increase in attenuation within the Percidae appears to be primarily or entirely associated with the elongation of the vertebral centra, rather than with an increase in vertebral number; deepening of the body is marked by some foreshortening of the vertebrae. Barlow (1961) reacted skeptically to the idea that the addition or subtraction of a few elements would be of selective value. However, as in the Percidae, vertebral number in the species of *Peprilus* seems to be significantly associated

with size and body shape (Table 21). Size of individual vertebrae seems to be about the same among the species.

P. snyderi, the most elongate and probably the largest species in the genus, has the greatest number of vertebrae, 36. *P. paru*, the deepest-bodied of the species, and also considered to be the most highly derived member of the genus, has the fewest vertebrae, 29 to 31. The close relative of *P. paru* in the Pacific, *P. medius*, is a more elongate species and has 33 to 35 vertebrae. *P. ovatus*, the deep-bodied, small derivative of *P. medius*, has 31 to 33 vertebrae. The relatively elongate *P. triacanthus* has 31 to 33 vertebrae while its close but slightly deeper, smaller relative, *P. burti*, has 29 to 31. The only exception to the trend occurs in *P. simillimus*, a relatively elongate species, which has 30 or 31 vertebrae. Vertebral number in association with other character trends appears to have selective value in the genus, and this selection apparently reduces the variability of the character.

In stromateoid evolution the general tendency has been toward an increase in the number of vertebrae (Haedrich, 1967). This trend seems to have culminated in the rather high number among the Stromateidae. However, from the basal stromateid stock the trend in *Peprilus* seems to be toward a reduction in number of vertebrae in correlation with the trend toward a deep, less elongate body.

Body form; shape, position, and loss of fins. Body form is associated with the shape and position of the fins and both in turn are associated with the locomotion and mode of life of the fish. Myers (1958), Liem (1963), and Patterson (1964) have stated and presented evidence that within the teleostean fishes and particularly the acanthopterygians there has been a trend toward a shorter, deeper, more highly compressed body. Associated with this trend have been several changes in skeletal features and in the shape and location of the fins.

The Stromateidae represent the zenith of stromateoid evolution (Haedrich, 1967) and are among the smallest fishes of the suborder. Within the Stromateidae, particularly the genus *Peprilus*, a number of specific conditions and trends exemplify some of the general tendencies occurring in acanthopterygian fishes.

All species of *Peprilus* are relatively deep, varying from elongate to very deep, and are highly compressed. A trend in spiny-rayed fishes has been for the pectoral fins to move to a lateral position on the body and for the pelvic fins to migrate forward from an abdominal position. The pectoral fin in a lateral position has assumed the primary functions of braking and turning (Harris, 1937; Patterson, 1964). The braking movements of the pectoral produces a lift as well as a drag force. Harris (1937) has shown that the neutralization of this lift force is effected by an equal downward force produced by the anteriorly-placed pelvic fins. If migration of the pelvics had not occurred in evolution along with the migration upward of the pectorals, the fish would either tilt upwards or rise bodily when it comes to a stop.

Extension of a pectoral facilitates turning; and turning is most rapid if the mass is concentrated at the level of the pectorals, the fulcra in turning (Patterson, 1964). Such a concentration of mass can be achieved by deepening the body, and for retention of streamlined form, greatest depth is required about at the level of the pectoral.

The dorsal and anal fins function to stabilize against rolling motion, i. e., they serve primarily as keels (Breder, 1926; Harris, 1937). A fish inclined to roll will do so about the long axis of the body; thus, for the dorsal and anal fins to be most effective they need to be as far as possible from the long axis. If the body is deepened, the dorsal and anal fins are farther from the long axis, and rolling stability is increased.

That the pelvic fins act as bilge keels has been advocated by Breder (1926). Harris (1937) differs and states that the pelvics may be used rather to produce rolling movements for establishing equilibrium or for swimming between rocks or into crevices in other than an upright position.

The swimming behavior of adults of three species, *P. triacanthus, P. burti,* and *P. paru,* was observed in this study. In each instance the fishes were accustomed to the tank and locomotion was apparently normal. All species were observed in public aquaria or in tanks in which I had placed freshly collected fish. Swimming appears to be a continuous process with no hovering in midwater. Locomotion is partially produced by the usual serial contractions of myomeres, but propulsion by the flapping of the pectoral fins is also well developed, especially at less than maximum speeds. Fishes of this genus appear to be moderately rapid swimmers with the ability for quick turning and for continuous swimming for long periods of time.

Pelvic fins are present in only one species of the Stromateidae, in specimens smaller than 100 mm SL of *Stromateus fiatola* (Haedrich, 1967). Other stromateoids have pelvic fins that are generally situated under the pectorals; the pelvics are very large in *Nomeus.* The loss of pelvic fins might seem to be a major evolutionary change. A rather specific geometric and hydrodynamic condition of the body in relation to swimming and mode of life of the fish should exist or develop if a species or group of species can dispense with a set of paired appendages. In S. *fiatola* the pelvics are apparently in the process of being lost, and in the other stromateids these fins have already been lost. In several groups of perciform fishes pelvic fins are quite small and in some they are absent. The actual form of the pelvic fins appears to be of little significance in rapid swimming, these fins being no more than maneuvering devices and often following the form of the pectorals. The pelvics are the fins most commonly modified so as to lose all locomotor function. The following discussion considers the loss of the pelvics only in the stromateid fishes, but may also apply to certain other perciform groups.

The position and function of the pectorals, the shape of the body, and the mode of swimming all should be relevant to the loss of the pelvics. In *Peprilus* the pectorals appear to perform at least three functions: braking, turning, and propelling. Propulsion is of the carangiform type, supplemented by the synchronous flapping of the pectoral fins. The latter is more important at lower speeds. This use of the pectorals is common in short, deep-bodied forms, according to Breder (1926).

Breder stated that with the development of a short, deep, compressed body, and a centrally-located pectoral, may come a reduction or loss of pelvic fins – as in the genus *Vomer* (Carangidae) or in *Peprilus triacanthus. Vomer* is a deep, extremely compressed pelagic fish with very small pelvics which seem, certainly, to be of little functional importance. *P. triacanthus* is also a deep, highly compressed pelagic fish, the adults of which swim continuously without hovering. If frequent braking does not occur, as seems to be the case in *Peprilus,* less of a downward force is needed or less frequently needed to counteract the lift force created by the pectorals in braking. Also, the deep portion of the body beneath the pectorals should provide some downward force which would further reduce the need for pelvic fins. Breder reasoned that the pelvics may be large, as in the somewhat primitive perciform genus, *Lepomis* (Centrarchidae), which frequently stops and hovers.

Fishes of the genus *Peprilus* appear to possess several attributes for moderately rapid swimming at least for short periods. The caudal fin is deeply forked. Gero (1952) has demonstrated that the tips of the caudal fin produce less turbulence than

the center portion. Thus, the more deeply forked the fin, the less should its oscillations disturb the water. As the aspect ratio (= (span of the fin)^2/area of the fin) is increased the drag diminishes. Aspect ratios of *Peprilus* range from about 3.5 in *P. simillimus* to about 5.0 or more in *P. medius*, which puts the group into the upper range or above of Nursall's (1958) category of "typical fish." This category includes fish which have moderate amplitude and fairly high frequency waves to form swimming oscillations, a flexible vertebral column of 24 to 100 vertebrae, a definitely narrowed but muscular caudal peduncle, and a flexible, forked tail of intermediate aspect ratio (two to four).

Breder (1926) stated that pectorals of spatulate or fanlike form accompany fishes of slow or moderate speeds, while long and falcate ones accompany rapid swimmers. The rapid swimmers were said to use such fins largely for quick-turning and seldom, if ever, for either propulsion or for maintaining a stationary position. The above does not agree with the condition in *Peprilus* in which the pectorals of large juveniles and adults are long and winglike, but are used in propulsion.

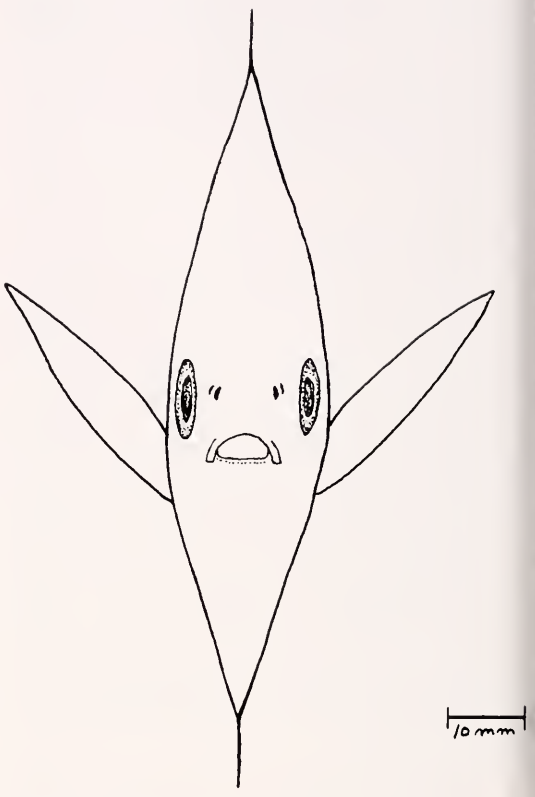


Figure 29. Frontal view of *Peprilus paru*, 117.0 mm SL specimen.

One function of the dorsal and anal fins is to produce stability against rolling (Breder, 1926; Harris, 1937). The cross section of many fish, including *Peprilus*, is elliptical at the level of the pectoral fins (Fig. 29). The corresponding position of maximum tangential velocity during rolling movements are not at the sides, but at the top and the bottom of the body, the positions of the dorsal and anal fins. The dorsal and anal fins of rapidly swimming fish are often somewhat similar in size and shape, especially in the latter. Frequently in less active forms, one fin may be larger than the other. A trend or at least a morphological arrangement mentioned by Breder (1926) which seems to be operative in *Peprilus* is that in reasonably elongate forms that have the pelvic fins greatly reduced or wanting, the anal fin is usually quite long with the vent displaced forward and the first interhaemal directed backward. Another observation of Breder which seems to have some relevance in the genus *Peprilus* is that of the relation of the development of the dorsal and anal fins to the area of concentration of the bulk of the body. Breder (1926) observed that in fishes with their greater bulk above a line from the tip of the snout to the middle of the peduncle, the dorsal fin is generally larger than the anal. And conversely, when the bulk is below that line, the anal fin is generally the larger. In fishes nearly symmetrical about such a line, the dorsal and anal fins are nearly equal in size. Five species of *Peprilus, P. snyderi, P. simili-*

mus, *P. triacanthus*, *P. burti*, and *P. medius*, have the greater bulk above the line and all have dorsal fins which are longer (more rays) than the anal fins (Table 21). *P. paru* has slightly greater bulk above the line and has only a slightly longer dorsal than anal fin (Table 21), while the anal is usually more falcate. *P. ovatus* is nearly symmetrical about this longitudinal line and, in turn, the dorsal and anal fins are very similar in size and shape (Table 21); the mean ray counts are about equal (D, 42.8; A, 43.0). The above pattern suggests that selection favors the size and positioning of these steadying keels which provide the optimum range of stability. The extremely long anterior lobes of the dorsal and anal fins of *P. paru* and *P. medius* may serve to increase rolling stability in these deep-bodied fishes, and the anal lobes may somewhat replace the pelvic fin in producing a downward force in counteraction to the upward force produced by the pectoral fin.

Patterson (1964) has stated that during teleost evolution the number of precaudal vertebrae has been reduced more drastically than the number of caudal vertebrae. This feature is characteristic of stromateoid fishes. The results of this change in proportion, according to Patterson, is that in acanthopterygian fishes the less muscular abdominal region is reduced more than the highly muscular and propulsive caudal region, and the resistance to lateral oscillation of the anterior part of the fish is reduced. These trends can be compensated for by increasing the depth of the trunk, for the streamlined form of the fish demands that the greatest depth be anterior to the point of contraction in oscillating the tail. The most elongate species, *P. snyderi*, has 15 precaudal and 21 caudal vertebrae; the shorter, deeper species of *Peprilus* have 13 precaudal and as few as 16 caudal vertebrae.

Swimbladder and mode of life. Changes in the mode of life during development are probably closely correlated with the size and shape of the pectoral fins and with the state of the swimbladder.

The larvae and small juveniles of *Peprilus* are surface dwellers after hatching in offshore waters. They then generally migrate to coastal waters and bays. At a length of about 10 to 30 mm SL, the young frequently become associated with jellyfish medusae and may maintain such a relationship up to a size of 80 to 100 mm SL. This association is well documented (Pearson, 1941; Bigelow and Schroeder, 1953; Mansueti, 1963; and others), and appears to be an important aspect of the life history.

The young fish apparently seek protection among the coelenterate tentacles and also feed on the tentacles themselves. Mansueti (1963) has shown in laboratory experiments that the association requires of the fishes an ability to hover, a locomotor attribute not evident in adult *Peprilus*. The adults that I have observed (three species) swim continuously with little or no hovering in midwater.

Two characteristic changes seem to correlate with the above apparent shift in habit and locomotor pattern. The first is the change of the pectoral fin from a short, fanlike structure to a long, winglike one. The change begins early and continues until the fish reaches a size of 80 to 100 mm SL (Figs. 9, 11, 15, 17, 20, 23, and 28). The second change is the apparent regression of the swimbladder in individuals larger than 80 to 100 mm SL. Although the information is from only three species, *P. triacanthus*, *P. burti*, and *P. paru*, a swimbladder is present in these fishes up to at least a size of about 100 mm SL. The organ is elongate, thin-walled, and slightly inclined anteriorly. In adult specimens of all species no swimbladder has been found, although fresh or well-preserved material of every species has not been examined. It seems, then, that the swimbladder becomes regressed and nonfunctional in fishes larger than 100 mm SL. It may be that the swimbladder is functional in juveniles and important in hovering and maintaining position

Table 21. Associations and Trends of Certain Character Values Among the Species of *Peprilus*. The deepest-bodied species is listed at left followed in order of decreasing body depth by the other species. Mean morphometric values are in thousandths of SL.

	paru	*ovatus*	*burti*	*medius*	*simillimus*	*triacanthus*	*snyderi*
Body depth	710	619	551	529	461	458	427
Preanal distance	484	481	465	434	440	445	424
Predorsal distance I	435	408	395	390	369	381	364
Caudal peduncle depth	092	079	075	078	065	070	071
Eye diameter	103	093	100	082	073	086	070
Pectoral fin length	386	360	332	386	336	312	329
Mean total vertebrae	30.0	32.0	30.0	34.0	30.2	31.7	36.0
Ratio of dorsal rays to anal rays	1.04	1.00	1.10	1.06	1.13	1.10	1.11
Relative length of anterior lobes of median fins*	1	3	4	2	6	4	5

* Longest lobes given rank of 1.

under floating objects such as jellyfish medusae, and that the organ becomes nonfunctional when swimming becomes continuous.

Jordan and Evermann (1896) indicated that the swimbladder is "usually" absent in stromateid fishes. Breder (1926), in discussing the hydrostatic situation for fishes which lack a swimbladder, stated that some fishes such as *P. triacanthus* (indicating that this fish has no swimbladder) are so close to the specific gravity of water due to a sufficient amount of fat, that only the slightest movement suffices to keep them from sinking or rising. Fishes of this genus are quite oily and perhaps this condition does facilitate the maintenance of position and the ease of ascent or descent. I have observed the movements of adult *P. triacanthus* in aquaria, and it appears that slow sinking follows cessation of active swimming, but that only the slightest pectoral movements return the fish to a horizontal or an upward direction. H. F. Taylor (1922) calculated that absence of a swimbladder in other than bottom forms should occur only in marine fishes since the quantity of fat necessary to float a fish in the less dense fresh water is practically prohibitive. He estimated that a marine fish with a fat content of 29.34 per cent and with no swimbladder would be in equilibrium with sea water. Many other factors, however, including the relative amount and density of bone need to be considered in this situation.

N. B. Marshall (personal communication) states that a number of shallow-water marine fishes have regressed, age-dependent swimbladders. He includes in the list certain gobies, blennies, flatfishes, certain *Solenichthys* spp., most muraenid eels, gadids such as *Gaidropsarus* spp., and some percomorphs such as *Thalassoma bifasciatum*, *Holacanthus tricolor*, *Upeneus prayensis* and an oceanic species, *Nomeus gronovii*. The latter species is a stromateoid and lives closely associated with the siphonophore, *Physalia*. Whether *Nomeus* stays with *Physalia* all its life is uncertain. The familiar small, blotched *Nomeus* found under *Physalia* may only be the young form of a bigger fish which lives in deep water. In *Nomeus*, as in *Peprilus*, regression of the swimbladder may correlate with a change in mode of life.

The above discussion of swimbladder loss is speculative at this stage. A number of questions remain to be resolved. Further examination of specimens, observations of living fish, and a series of experiments are being planned in an attempt to answer some of the questions. A comparative study of stromateoids and other fishes with

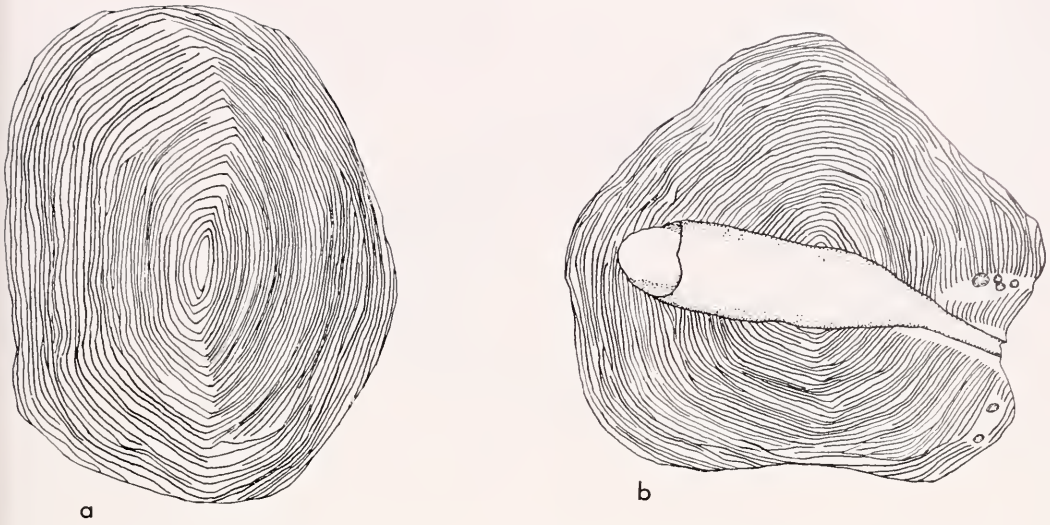


Figure 30. Scales of *Peprilus snyderi*: a = scale from trunk below lateral line; b = lateral line scale from mid-trunk region. From 227.0 mm SL specimen.

regressed, age-dependent swimbladders is being initiated.

Character associations. Listed in Table 21 are the mean values of some morphometric and meristic characters which illustrate trends in sets of characters among the species of *Peprilus*. *P. paru*, the shortest, deepest-bodied species, is listed first in the table, followed in order by the more elongate species. From this ranking the table shows how other characters relate to that of body depth. Greatest body depth is associated with the greatest preanal and predorsal distances, the longest pectoral, the largest eye, and the fewest vertebrae. In the most elongate species, *P. snyderi*, these character values are largely reversed. *P. snyderi* probably does not have the quick-turning ability attained by *P. paru* or *P. ovatus*, for example.

I have not analyzed unit characters or their roles by the techniques of Olson (1964), although this approach might be instructive, especially if applied to the entire suborder.

Skin and scales. The skin of *Peprilus* is thin and, as in most other stromateoid fishes, the scales (Fig. 30) are thin, cycloid, irregular in shape, highly deciduous, and in shallow pockets in the skin. The lateral line scales (Fig. 30b) have a simple tube passing through the middle, and are less deciduous than scales of other parts of the body. The scale condition in *Peprilus* may be important in achieving greater maneuverability and may represent a stage in a trend toward complete loss of scales. The cephalic lateral line consists of pores and branching canals on the cheek, opercular area, snout, lower jaw, and top of head.

In the stromateoid fishes there is usually a well-developed subdermal canal system which communicates to the surface through small pores scattered over the head and body (Haedrich, 1967). The system is particularly well developed in *Peprilus* (Fig. 31), and is conspicuous in living or freshly collected fish. The canals often are only slightly visible after preservation. There are some differences in the system among the species of the genus. *P. burti* and *P. triacanthus* (Fig. 19 and 21–22) have a row of large pores beneath the anterior half of the dorsal fin. A series of

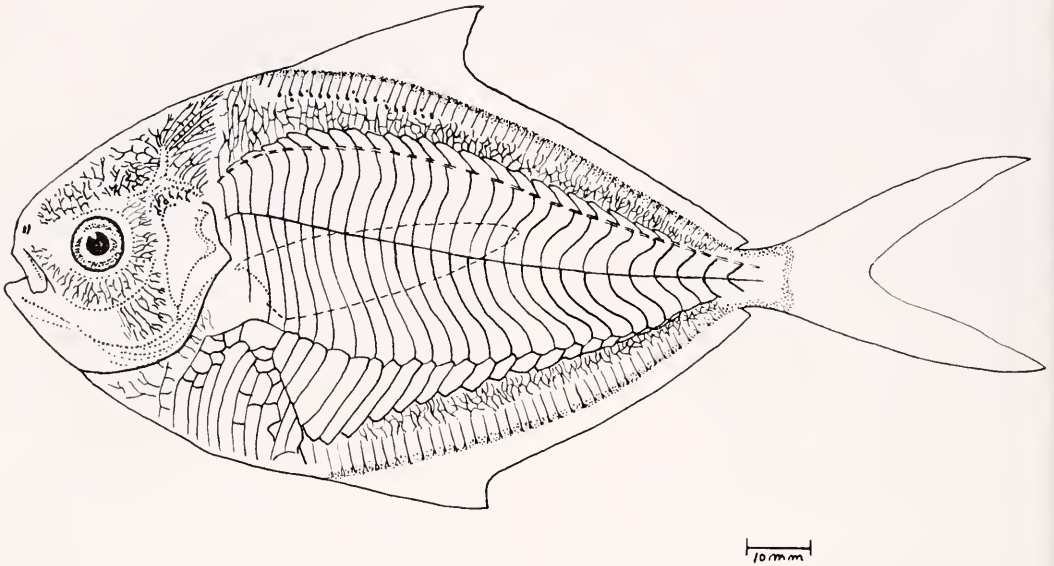


Figure 31. Subdermal canal system and portions of the cephalic lateral line of *Peprilus burti,* 124.6 mm SL specimen.

small, irregularly-spaced, but conspicuous pores are sometimes evident along the dorsal surface of *P. ovatus* (Fig. 10).

The function of this extensive canal system is unknown. Whether the system is independent of the lateral line and whether sensory structures are present are unknown. If the canals contain a sensory mechanism, they may function as receptors important in the formation and maintenance of schools. These fishes produce large amounts of mucous, and the system might be used in the dispersal of the mucous which may contain an agent that counteracts coelenterate toxins. Walters (1963), in a study of the integument and subdermal canal system of the trachipterid fishes, has proposed that the canal system functions in boundary-layer control through distributed dynamic damping. Such control could apparently decrease drag by 60 to 75 per cent. According to the hypothesis, as the skin pressure mounts beneath a growing boundary-layer perturbation, the layer will sink through the surface pores to enter the subdermal canals; the canal fluid will simultaneously flow toward regions of lower pressure and re-enter the boundary layer through the surface pores. This simultaneous series of events would dynamically damp the disturbance. Walters also found similar integuments in two species of Gempylidae. LaMonte (1958) reported that the skin of marlin, genus *Makaira,* has many minute, round openings. Whether such a system operates in *Peprilus* or in gempylids and marlin is unknown. Metabolic economy in *Peprilus* does not seem critical, and selection pressure for such a mechanism would not appear to be great. However, all the above possibilities as to function remain in question, and further investigation is required.

Alimentary canal. The alimentary canal with its several elaborations (Fig. 32) suggests that feeding and food conversion are rather specialized. Each part of the canal is considered below, and an attempt is made to correlate the part with its probable function.

The jaw teeth (Fig. 33) are small, uni-

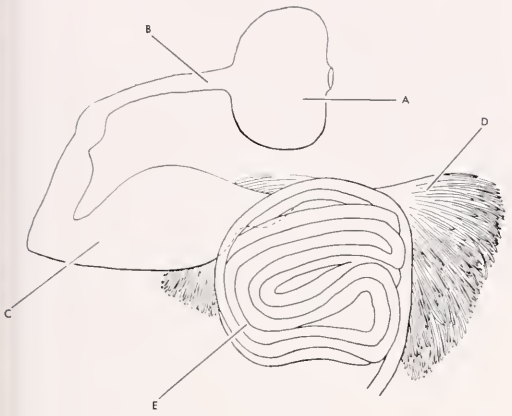


Figure 32. Alimentary canal of *Peprilus paru*: A = pharyngeal sac; B = esophagus; C = stomach; D = pyloric caeca; E = intestine. From 124.6 mm SL specimen (semi-diagrammatic).

serial, and laterally compressed. The teeth of the upper jaw are slightly recurved, either simple and pointed (Fig. 33a), or have three small cusps (Fig. 33b). The teeth of the lower jaw are similar to those of the upper, but have either three cusps (Fig. 33a), or four or five cusps (Fig. 33b), and are not recurved.

The jaw apparatus seems suited for nipping parts from larger objects or for taking small objects whole. The significance of the differences in cusp pattern of the premaxillary teeth among the species of *Peprilus* is unknown. No teeth are present on the vomer, palatines, or basibranchials.

The gill rakers are long, slender, closely spaced, and beset with small teeth. They appear to serve as an effective screen in preventing small food particles from entering the gill area or from escaping through the opercular opening. However, they do not appear to serve as a straining device. Small differences in the number of gill rakers among the species of *Peprilus* do not seem sufficient to indicate differences in food habits.

The suborder Stromateoidei is characterized by toothed pharyngeal sacs located immediately behind the last gill arch. Bühler (1930) showed the sacs to be of

Figure 33. Jaws and teeth of two species of *Peprilus*: A = *P. paru*; B = *P. burti*; 1 = tooth of upper jaw; 2 = tooth of lower jaw. From cleared-and-stained specimens.

pharyngeal origin and worked out the morphology of them in two stromateoid families, the Centrolophidae and the Stromateidae. Haedrich (1967) has studied in detail the comparative structure of the sacs in the five stromateoid families. The

sac has muscular walls and appears to function as a shredding or grinding organ; and stomach contents are often shredded beyond recognition.

Immediately posterior to the pharyngeal sac is the short and thick-walled esophagus.

The stomach is a distinct, thick-walled, muscular, and roughly U-shaped organ which is capable of considerable distension.

The intestine is long, about two and one-half to three times the length of the body in *Peprilus*, and arranged into long loops in the body cavity. The intestine of fishes is generally considered to be the site of absorption. At the anterior end of the intestine is a dendritic mass of pyloric caeca. These structures, which develop as blind outgrowths of the anterior end of the intestine, are present in a number of families of teleost fishes. The number of caeca may vary greatly, from one to more than 1000 (Suyehiro, 1942). Suyehiro estimates there to be about 600 in the stromateid fish, *Pampus argenteus*. There are several hundred long, narrow caeca in *Peprilus*. It has been suggested (Al-Hussaini, 1947; Barrington, 1957) that the caeca are merely an adaptation which increases the surface area of the intestinal epithelium of fish in which the size of the body cavity limits the length of the intestine itself, or whose habits are carnivorous. Both of these criteria apply to *Peprilus*. The body cavity is small, probably because of other selection pressures for a short, compressed body. The fishes are also carnivorous, but there is no close correlation between gut length and food habits.

Food of *Peprilus* appears to consist of not only jellyfish but also small fishes, a variety of small crustaceans, and other small invertebrates. The pharyngeal sac is formed very early in life, at least by a size of 10 mm SL, and the young apparently feed in a manner similar to the adults. Juvenile *Peprilus* may eat proportionately more jellyfish than do the adults.

ASPECTS OF LIFE HISTORY AND ECOLOGY

Emphasis here is placed upon the four better known species, *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus*. Little is known of the life history of the other three species. It seems reasonably certain that the overall biology of the latter species will prove not to be substantially different from that of the other species. The fishes of this genus are similar and wherever they occur fill a similar niche in the ecosystem.

Early life history. The testes, ovaries, and eggs are similar among all the species. Dioecy seems to be the rule in the genus. Eggs are buoyant, transparent, spherical, and contain one or more oil globules. Egg diameters range from 0.75 to 0.79 mm in *P. triacanthus*, and 70 per cent of the eggs have a single oil globule (Colton and Honey, 1963). They reported that other eggs had two or three smaller oil globules. Eggs of *P. paru* in Chesapeake Bay are approximately 1 mm in diameter (Hildebrand and Schroeder, 1927). Ovaries in a ripe fish occupy more than one-half of the body cavity. Maturity is reached in *P. triacanthus* at about two years of age (Bigelow and Schroeder, 1953), and at a length of about 140 to 180 mm SL; however, I have examined nearly ripe individuals which were as small as 120 mm SL. The size at maturity of the smaller species such as *P. burti* and *P. ovatus* is probably less than that for *P. triacanthus*. Hatching time for *P. triacanthus* is around 48 to 72 hours, and size of larvae at hatching is slightly less than 2 mm (Pearson, 1941; Colton and Honey, 1963).

The identification of larval *P. triacanthus* and *Urophycis chuss*, the squirrel hake, has been confused. Pearson (1941) and Miller and Marak (1959) indicate that the early larval stages considered by Kuntz and Radcliffe (1918) to be *P. triacanthus* are those of *Urophycis chuss*. Colton and Honey (1963) have shown that eggs of *P. triacanthus* differ from those of *U. chuss*

described by Hildebrand and Cable (1934).

Spawning generally occurs in the spring and early summer, although the period of spawning may be longer in some of the warm-water species. Bigelow and Schroeder (1953) indicate that spawning of *P. triacanthus* in the Gulf of Maine begins in June, is at a maximum in July, and continues into August. Pearson (1941), on the basis of appearance of larvae, postulated a late spring and early summer spawning for *P. triacanthus* and *P. paru* in lower Chesapeake Bay. *P. paru* in the Gulf of Mexico apparently spawns in the spring (J. M. Miller, 1965). On the basis of the occurrence of young in winter and spring, Miller suggested a winter and possibly an autumn spawning for *P. burti.*

The type of eggs, the seasonal distribution of mature individuals, and the larval distribution should give some indication of the area of spawning. The eggs are buoyant and transparent which indicates that they are pelagic and near the surface. Kuntz and Radcliffe (1918), and Bigelow and Schroeder (1953), stated that spawning in *P. triacanthus* occurs a few miles offshore. Mature individuals are known to leave inshore waters during the spawning season, and those returning later are spent. Schaefer (1967) reported that *P. triacanthus* of spawning size does not appear in the surf zone until June, which indicates that before this time the fish were offshore. According to Miller (1965), *P. burti* moves offshore with increasing water temperatures in the spring, which indicates that spawning is offshore. Data from M/V GILL cruises along the coast of the southeastern United States show that *Peprilus* sp. larvae are several miles offshore. Larvae of *P. simillimus* occur both near shore and several miles offshore, but generally in large protected areas (Fig. 39). Offshore concentrations of both larvae and mature fish of this species suggest that spawning is generally a few miles offshore in surface waters.

Almost nothing is known of the spawning act. Aggregations of mature fish probably develop in offshore waters followed by mass extrusion of reproductive products. There is probably little courtship behavior before the spawning act. No external sexual dimorphism has been detected except the distension of the abdomen of ripe females. Segregation of males and females is not known to occur; large collections usually contain both sexes in reasonably equal numbers.

The eggs and early larval stages are in the surface layers and constitute part of the plankton. Ahlstrom (1959) stated that larvae of *P. simillimus* occurs between the surface and a depth of 48 m. Plankton volume data of the California Current Survey (Staff, South Pacific Fishery Investigations, 1956; Thrailkill, 1957, 1959, 1961, and 1963), in combination with information supplied by Dr. Ahlstrom, show that the larvae of *P. simillimus* are in the surface layers usually at depths of 50 m or less. Larvae which I identified as *Peprilus* sp. and which were taken on M/V GILL cruises off Georgia and South Carolina were in the surface layers to a depth of 72 m.

Distribution of larvae of *P. simillimus* on the Pacific coast (Fig. 39) is mostly near shore and in bays or other protected areas, although many were collected at considerable distances from shore. The greatest numbers of larvae are taken mainly around Cedros Island and Bahía Sebastián Vizcaíno off upper central Baja California, and smaller concentrations are taken in the Channel Island area near Los Angeles and near Bahía Magdalena off lower central Baja California (Figs. 39 and 40). Bigelow and Schroeder (1953) stated that although a considerable number of eggs of *P. triacanthus* are produced in the Gulf of Maine, very few larvae are taken there. They reported that no young *P. triacanthus* have been taken in the Bay of Fundy, but that they are very plentiful along the shores of southern New England. That juveniles of

Peprilus occur in bays and other inshore areas during the summer has also been shown by Reid (1955) for *P. paru* in Texas, Mansueti (1963) for *P. paru* and *P. triacanthus* in Chesapeake Bay, and by Schaefer (1967) for *P. triacanthus* in the surf zone of Long Island, New York.

In summary, the young of *Peprilus* appear to move inshore after hatching in pelagic surface waters to bays and other protected areas which serve as favorable nursery grounds. This general inshore movement coincides with the presence and abundance of certain coelenterates with which the young fishes of this genus associate in the summer and early fall (Mansueti, 1963).

Distribution in relation to certain physical factors.

Temperature. Temperature is probably the most significant factor affecting the distribution of members of the genus *Peprilus.*

Stromateids are basically warm-water fishes and secondarily have invaded temperate regions. *Stromateus* off southern South America and off southern Africa, and *Peprilus* in the western North Atlantic off Newfoundland and in the eastern North Pacific off British Columbia, represent the farthest penetrations into temperate waters.

Peprilus in its most northerly range is not abundant and generally is regarded as a summer visitor. Even though limited by temperature, some members of the genus do occur over a wide range of temperature. *P. triacanthus* off the northeastern United States is found where bottom temperatures range in autumn from 4.4° to 20.6°C (Fritz, 1965). Data from groundfish surveys (Figs. 34–36) off the northeastern United States show that *P. triacanthus* has been taken over areas where the mean bottom temperatures ranged from 5.0° to 14.2°C, these figures representing the total range for summer, autumn, and winter for the years 1963 to 1966. Schaefer (1967) has collected *P. triacanthus* in the surf zone of Long Island in August in water temperatures as high as 21.6°C. *P. burti,* a close relative of *P. triacanthus,* has been taken in waters of temperatures as high as 28°C and as low as 12.6°C (Gunter, 1945). *P. paru* has been collected in waters ranging in temperature from 13.7° to 30.0°C (Gunter, 1945) and from 14.6° to 27.5°C (J. M. Miller, 1965). *P. paru* is a shallow-water species, usually in waters of less than 50 m depth, and probably does not encounter as wide a range of temperatures as does *P. triacanthus. P. simillimus* on the Pacific coast probably encounters a range of temperatures similar to that of *P. triacanthus* since their latitudinal distributions are complementary.

The largely tropical and subtropical species of the Pacific, *P. medius, P. ovatus,* and *P. snyderi,* are almost certainly limited to a narrower, warmer range of temperatures than the above species.

Salinity. The habit of entering bays and even river mouths indicates that members of this genus are euryhaline. Reid (1955) collected a juvenile *P. paru* at a bayou mouth in a salinity of 10.3 ppm and two others at salinities of 17.3 and 17.6 ppm. Schultz (1962) collected *P. paru* in Texas bays in salinities ranging from 18.9 to 19.5 ppm. Gunter (1945) caught *P. paru* in the Gulf of Mexico in high salinities, 33.0 to 36.7 ppm. *P. burti* has also been collected in waters of widely varying salinity. Gunter (1945) reported that *P. burti* occurs in a salinity range of 15.6 to 35.2 ppm, but mainly in salinities over 30 ppm. Schultz (1962) gave a range of 21.5 to 25.9 ppm for *P. burti* in Texas bays. Schaefer (1967) recorded a salinity range of about 29.0 to 33.0 ppm for the surf waters of Long Island in which *P. triacanthus* is an abundant species. *P. burti* and *P. paru* have both been collected in Lake Pontchartrain, Louisiana (Tulane University Collections), a lake of varying salinity. *P. ovatus* has been taken at the mouth of the Colorado River (SIO 63–484) in the northern Gulf of California.

Currents. It is possible to correlate ex-

isting current patterns with the distribution of almost every species of *Peprilus*. The influences of currents in the distribution of the species of *Peprilus* is discussed below in the section on zoogeography.

Sediment or bottom type. In general, members of the genus *Peprilus* are distributed either over a sand or a mud bottom or a combination of both. None of the species are residents of rocky shores or coral zones, though they may occur in such an area temporarily. The preference for either a sand or a mud bottom is not usually species specific.

P. triacanthus off the coast of the northeastern United States is usually distributed over a sandy bottom or a combination of silt and sand. Fritz (1965) showed that the autumn distribution of this species is over the latter type. Bigelow and Schroeder (1953) stated that this species has such a decided preference for sandy bottoms rather than for rocky or muddy bottoms that few are taken in traps on muddy ground, while other traps along a sandy beach may yield considerable numbers. Leim and Scott (1966) report that small schools of *P. triacanthus* occur over sandy bottoms along the Canadian coast during the warmer months. In the southern part of the range of *P. triacanthus* there appear to be two distinct populations: one primarily in deep water and distributed over a mud bottom; and the other in shallow, inshore water over a sand bottom (Table 22). Most of the shelf area off the southeastern United States is sandy with some small areas of mud and gravel (Moore and Gorsline, 1960). While there seems to be a preference of each apparent population for either a sand or a mud bottom, there is overlap and no strict segregation. The apparent existence of two distinct populations in the Atlantic off the southeastern states is discussed on p. 247.

P. burti of the Gulf of Mexico is most frequently distributed over a mud or a sand-silt bottom (Table 22).

There are few data on the other species. *P. ovatus* in the northern Gulf of California has been collected over mud and sand bottoms. *P. simillimus* is found over both sand and mud bottoms.

Depth. Fishes of this genus may be found in waters as deep as 420 m on the continental slope (Table 22), but more frequently are found in much shallower waters.

Fritz (1965) reported that *P. triacanthus* occurs in a depth range of 30 to 270 m off the northeastern United States, but stated that the species is most abundant in 50 to 90 m of water. Data for other seasons (Figs. 34, 36, and 37) do not expand the above depth range.

Table 22 gives the depth ranges of *P. triacanthus*, *P. paru*, and *P. burti* off the southeastern United States and in the Gulf of Mexico. As mentioned earlier in the discussion of sediment type, *P. triacanthus* in its southern distribution has a wide depth distribution correlated with the possible existence of two separate populations or species in that region. This species has been taken in depths ranging from 20 to 420 m off the southeastern coast of the United States. The closely related *P. burti* in the Gulf of Mexico has a less extensive depth range with greatest abundance at a range of about 9 to 135 m. *P. paru* is a relatively shallow-water form which occurs in inshore areas throughout the year.

The depth distribution of *P. simillimus* is probably similar to that of *P. triacanthus*.

There is little information on the vertical distribution of the tropical Pacific species. *P. snyderi*, *P. medius*, and *P. ovatus* have been taken in inshore areas in depths of less than about 50 m. *P. ovatus* probably does not occur beyond this depth while *P. snyderi* may descend to greater depths. *P. medius* seems to compliment in the Pacific the ecology of *P. paru* in the Atlantic; thus, its depth range may be similar to that of the latter species.

Seasonal distribution and abundance. Seasonal movements are generally characteristic of the more temperate species of

Table 22. Summary of the Depth of Capture and Associated Major Bottom Type of Collections of Three Species of *Peprilus* Made by the M/V OREGON and M/V SILVER BAY in the Southwestern North Atlantic (Cape Hatteras to Southern Florida), and in the Gulf of Mexico for the Years 1950 through 1966.

Species	Region	Depth Range (meters)	Bottom Type
P. paru	Atlantic	6–88	sand and/or mud
P. paru	Gulf of Mexico	2–115	sand and/or mud
P. burti	Gulf of Mexico	2–274	sand and/or mud; infrequently coral
P. triacanthus (deep-bodied)	Atlantic (generally inshore)	7–145	usually sand; less often gravel, mud, or mud and sand
P. triacanthus (shallow-bodied; often spotted)	Atlantic (generally further offshore)	20–420	usually mud; less often sand, coral, or mud and sand

the genus. Seasonal migrations apparently serve to maintain the species within a favorable range of environmental conditions.

The seasonal movements of *P. triacanthus* (the butterfish) have been generally recognized for some time. Bigelow and Schroeder (1953) indicated that while definite evidence is lacking, butterfish in the Gulf of Maine and southward seldom appeared to descend deeper than 25 to 55 m during the summer, and to spend the winter and early spring near bottom in depths down to about 180 to 210 m. Fritz (1965) showed that in the same area butterfish are in shallow, warm waters during autumn and are abundant at depths of 50 to 90 m and at a water temperature of 11°C. He suggested that the fish migrates northward into the Gulf of Maine during the summer months. Pearson (1932) reported that small quantities of butterfish have been trawled in offshore waters in winter in Virginia and North Carolina. Leim and Scott (1966) stated that small schools of butterfish occur over sandy bottoms along the Canadian coast during the period of warm water from May to November, but are offshore in depths to 100 fms (183 m) in the winter. Schaefer (1967) found that butterfish of a wide size-range occur in the surf zone of Long Island from June through October.

The distribution of *P. triacanthus* in summer, autumn, and winter over a three-year period in the Gulf of Maine and in coastal waters south to just beyond 40°N is presented in Figures 34 to 36. Length-frequency values of the total catch calculated from a sample length-frequency are given for each seasonal catch. Figure 37 shows the depth zones for the strata of this geographic region. The strata maps of Figures 34 through 37 were designed, described, and presented in extended form by Grosslein (1969).

P. triacanthus is widespread both in inshore waters and over deeper waters near the edge of the continental shelf in the summer months (Fig. 34). The fish occurs to a limited extent in the Gulf of Maine, especially in the southern portion. The greatest number of individuals were collected in strata nine and ten (Fig. 37), and in waters of less than 55 m in depth. The species was collected over an area in which the mean bottom temperatures ranged from 5.8° to 13.3°C and in waters ranging from 40 to 247 m in depth.

The autumn distribution (Fig. 35) is similar to that of the summer distribution.

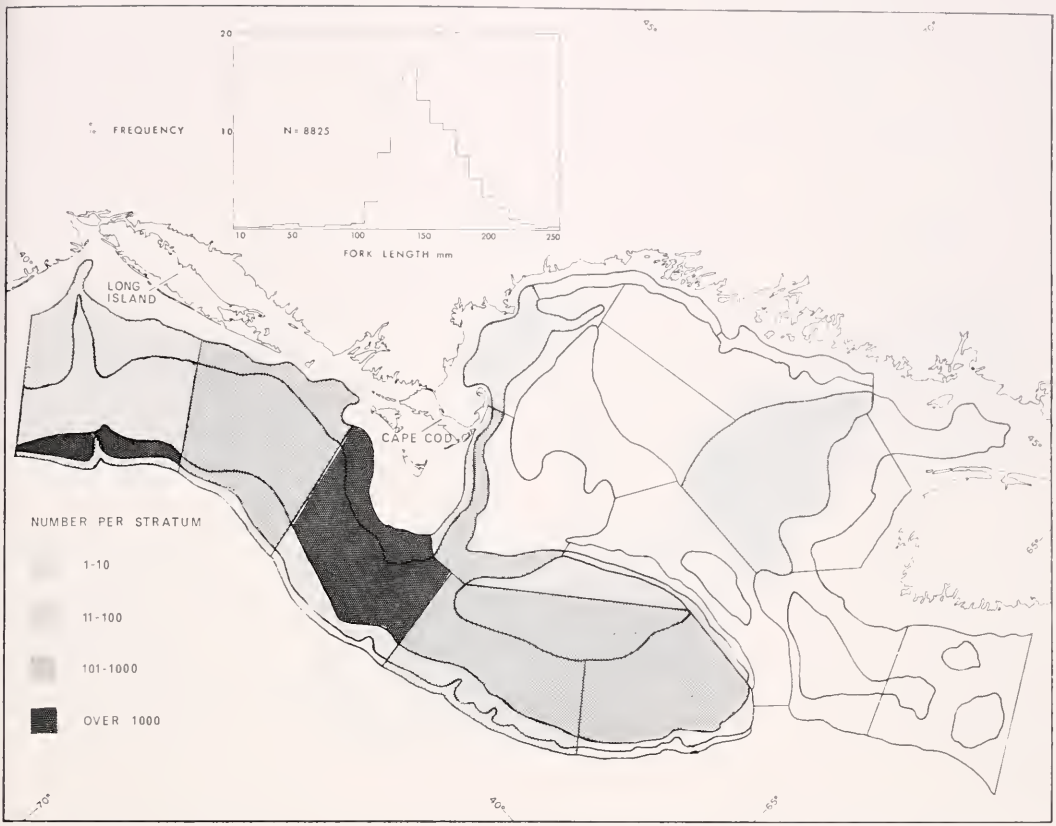


Figure 34. Summer (July and August) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1963–65. Data compiled from R/V ALBATROSS IV groundfish survey cruises of the U. S. Bureau of Commercial Fisheries, Woods Hole, Massachusetts. Number of fish per stratum is the cumulative total catch per stratum for the three-year period. Length-frequency is of the total catch calculated from the sample length-frequency; N = total catch of all strata for the three-year period. Strata map courtesy of Marvin D. Grosslein.

The greatest numbers of individuals were collected in stratum nine (Fig. 37), in waters of less than 110 m in depth. The species was collected over an area in which the mean bottom temperatures ranged from 5.8° to 14.2°C and in waters ranging from 33 to 250 m in depth.

The winter distribution (Fig. 36) is different from that of either the summer or the autumn. The winter collections made in the same region and with reasonably the same fishing effort, indicate that the species has a more restricted horizontal distribution during this season. The distribution is entirely south of the Gulf of Maine and in deep water. No fish were collected in the shallowest strata. The greatest numbers of individuals were captured in stratum seven (Fig. 37), in which the depth range is 112 to 183 m. Considerable numbers were collected in deeper water near the edge of the continental shelf. Collections were made over an area in which the mean bottom temperatures ranged from 5.0° to 10.2°C.

The spring distribution (no map, data for 1968 only) is similar to the winter distribution. The greatest numbers of individuals were collected in deep water along the edge of the continental shelf. The fish was

Figure 35. Autumn (October, November, and early December) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1963–65. Explanation of symbols and other information in Figure 34.

captured in waters ranging in depth from 44 to 274 m.

In the summer months along the coasts of the middle and northeastern Atlantic states, *P. tricanthus* has a wide, shallow-water distribution with movements both inshore and northward. The autumn distribution is similar. During the winter the species becomes restricted horizontally and concentrated in deep, offshore waters near the edge of the continental shelf. This winter concentration appears to be influenced strongly by water temperatures, and even though the seasonal distributions are different, the ranges of mean bottom temperatures strongly overlap for all seasons. The early spring distribution is similar to the winter distribution. In late spring, May to June, the species moves inshore and northward as upper level water temperatures begin to rise. The fish then assumes the summer distribution described above.

As spawning continues or is completed in late spring and summer, subadult and mature individuals of *P. triacanthus* range widely in shallow waters and occur in the surf zone from June through October on Long Island (Schaefer, 1967). Schaefer has shown that in June surf zone catches are mainly of large individuals, many of which are large enough to have already spawned offshore. In July, fish of a wider size-range are captured in the surf zone. The length-frequency diagram presented by Schaefer for August is bimodal with all

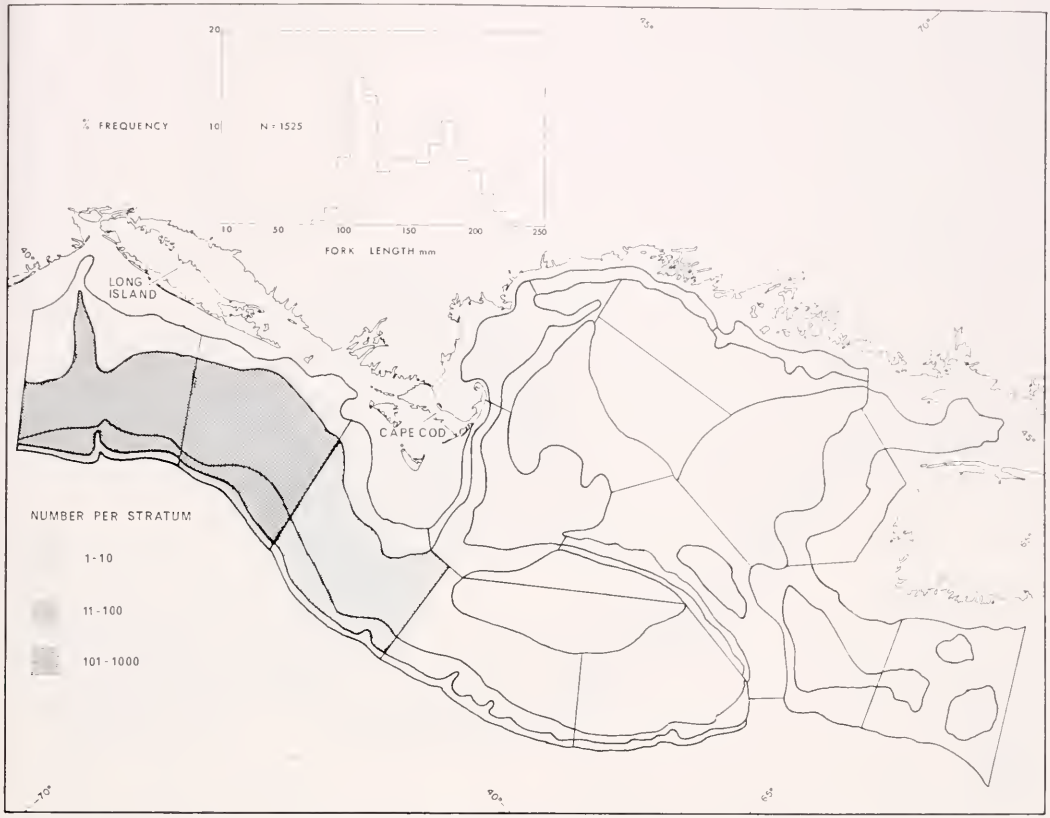


Figure 36. Winter (January and February) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1964–66. Explanation of symbols and other information in Figure 34.

fish of 100 mm FL (fork length in *P. triacanthus* approximately 10 per cent greater than SL) or less. This indicates that juveniles spawned earlier in the year are now entering the surf waters along with larger juveniles. Still larger fish were captured in August, September, or October. These large individuals probably move long distances during the summer and autumn even into waters as far north as Newfoundland and the Gulf of St. Lawrence.

The seasonal distributions and length-frequency diagrams (Figs. 34–36) do not include surf zone catches but only captures from trawlable waters. The length-frequency data seem to correlate well with Schaefer's (1967) data from the surf zone. In summer (Fig. 34), the diagram is essentially unimodal at around 140 mm FL, but it also indicates the presence of juveniles of 50 mm or less. All the fish were collected with a standard 36′ trawl having a one-half inch mesh codend liner; the use of a finer mesh probably would have resulted in the capture of more small fish. The data for autumn (Fig. 35) are weakly bimodal and consist mostly of large individuals of around 160 mm FL. This corresponds with the surf zone data which indicated that such large fish were absent from the surf in autumn. This further suggests that different size groups move independently, at least during the summer and autumn. The length-frequency diagram for winter (Fig. 36) is strongly bimodal with one peak around 100 mm,

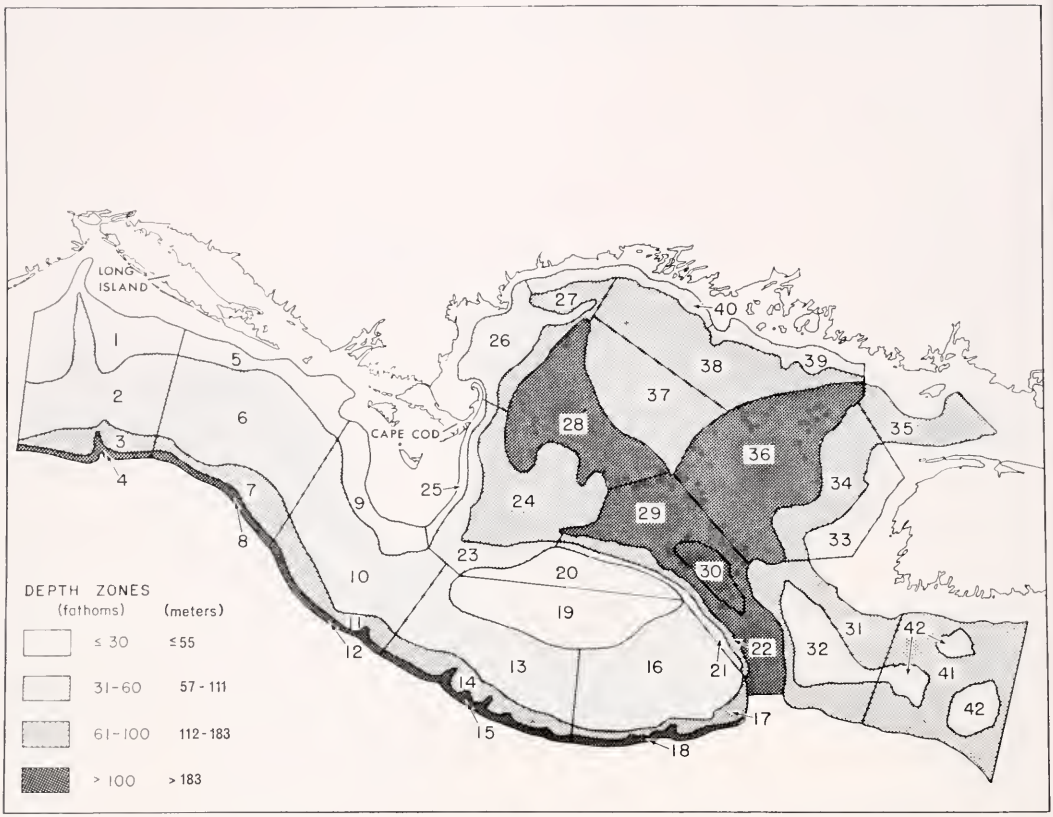


Figure 37. Strata map with depth zones corresponding to Figures 34 to 36.

another around 180 mm, and has a total size-range of 70 to 230 mm FL. The length-frequency diagram for the spring (Fig. 38) is similar to the one for winter. The curve is bimodal with one peak at around 100 mm and another at around 140 mm, but with many larger individuals. The total size-range is from 70 to 210 mm FL. These data for the winter and spring months indicate that two- and possibly three-year classes are concentrated in deep water during these seasons. Thus, there seem to be wide dispersal and independent movement of size-classes in the warmer months, and a concentration of a large part of the population in deep water in the colder months.

The seasonal distribution of *Stromateus maculatus* (=*Stromateus brasiliensis*) off the southern Atlantic coast of South America parallels in some respects that just described for *P. triacanthus* in the western North Atlantic. T. J. Hart (1946) described the main features of the seasonal movements of *S. maculatus* on the Patagonian shelf as follows: a double trend of seasonal movement – inshore in spring and summer with maximum concentration, offshore in autumn and winter with maximum dispersal; and, a meridional movement southward in summer and northward in winter. The latter aspect is similar to that of *P. triacanthus*, but, unlike the pattern of *S. maculatus*, maximum dispersal of *P. triacanthus* seems to occur in summer and autumn with maximum concentration in a restricted region occurring in the winter and early spring.

A number of fishes with warm-water af-

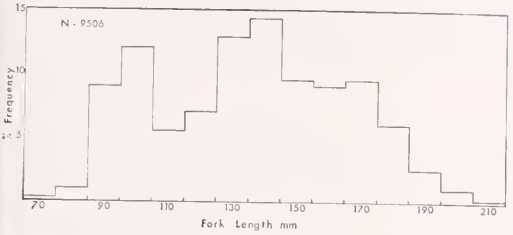


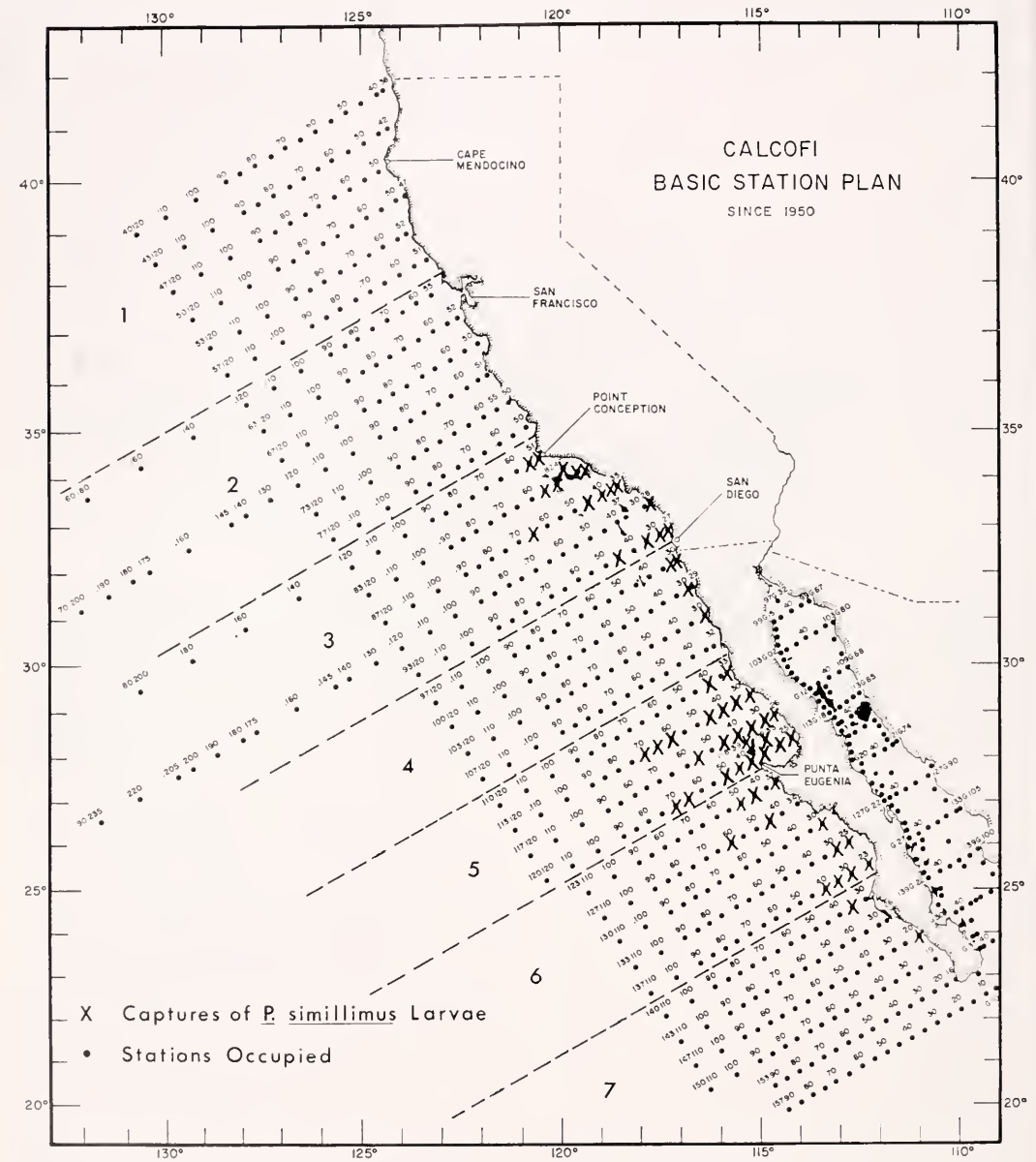
Figure 38. Length-frequency diagram for the spring (March, April, and early May) collection of butterfish, *Peprilus triacanthus*, made by R/V ALBATROSS IV groundfish survey cruises of the U. S. Bureau of Commercial Fisheries, Woods Hole, Massachusetts, off the northeastern coast of the United States, 1968. Length-frequency is of the total catch calculated from the sample length-frequency. See Figures 34 to 37.

finities migrate seasonally in a manner similar to *P. triacanthus*. Atlantic mackerel, *Scomber scombrus*, scup, *Stenotomus versicolor*, and weakfish, *Cynoscion regalis*, among others, migrate coastwards to their spawning grounds in spring and summer; before winter advances, when shallow, inshore waters become colder than those offshore, these species move offshore to warmer, deeper waters (Marshall, 1966). Whereas, cold-adapted fishes such as haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, may retreat in summer from warm, inshore waters to cooler, deeper reaches. Cape Cod is often recognized as the southern boundary of most boreal species and the northern boundary of many temperate species (Fritz, 1965). Some fishes are restricted to either north or south of Cape Cod while others range seasonally into the adjacent region. The distribution of *P. triacanthus* largely is south of Cape Cod except in the summer and autumn when it migrates northward into the Gulf of Maine. According to Fritz, Atlantic cod, *Gadus morhua*, a typical boreal species, may migrate as far south as Virginia during the winter months when temperature conditions are suitable. Silver hake, *Merluccius bilinearis*, and spiny dogfish, *Squalus acanthias*, for example, range widely both north and south of Cape Cod.

The other species of *Peprilus* which might be expected to migrate seasonally is *P. simillimus*, since it ranges into temperate waters as far north as the southern coast of British Columbia. Ulrey and Greeley (1928) reported that the fish is abundant in summer especially around Santa Cruz, California. Recent publications (J. L. Hart, 1949; Batts, 1960; High, 1966) have cited either the increased abundance or local occurrences of *P. simillimus* in Washington and British Columbia waters. Hart also pointed out that an increase in poundage of landings had occurred in the Monterey Bay area of California, whereas, previously, the major portion of the landings had occurred in southern California. Hart's list of occurrences of the species in British Columbia waters mostly includes records for the winter months of December, January, and February.

The distribution of *P. simillimus* larvae off the coasts of California and Baja California (Fig. 39) strongly suggests the warm-water affinities of the species. From 1955 to 1959, larvae of this fish have not been collected north of Point Conception, California, about 34°N. The greatest abundance of larvae was taken in the upper central Baja California area (Figs. 39 and 40), mainly around Bahía Sebastián Vizcaíno. Larvae were collected in greatest numbers in the months of May, June, and July (Fig. 41), although they were taken from January through August. There seems to be no significant time difference between the appearance of larvae in the northern (Point Conception) and in the southern (southern Baja California) parts of the distribution.

Berry and Perkins (1966), in a survey of the pelagic fishes of the California Current area from central California to central Baja California, reported that *P. simillimus* ranging in size from 12 to 165 mm SL occurred from Point Conception to the vicinity of Cedros Island near Bahía Sebastián Vizcaíno, Baja California. This distribution agrees closely with that of the larval distribution just described.



Figures 39. Distribution of larvae of *Peprilus simillimus* off the coasts of California and Baja California, 1955–59: 1 = northern California; 2 = central California; 3 = southern California; 4 = northern Baja California; 5 = upper central Baja California; 6 = lower central Baja California; 7 = southern Baja California. Data compiled from collections made by California Cooperative Oceanic Fisheries Investigations (CALCOFI). Map courtesy of Elbert H. Ahlstram.

Part of the adult population may move northward long distances along the Pacific coast during favorable periods. As has been mentioned, there have been reports of an increase in the northern abundance, yet the occurrence is still of sufficient novelty that reports continue to be published of the fish's capture in such northern

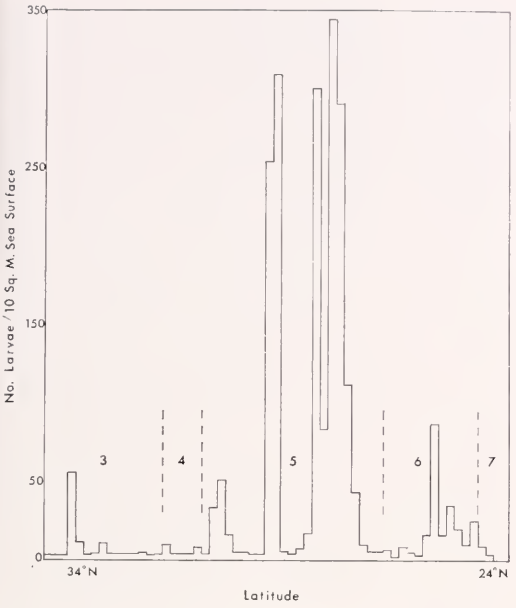


Figure 40. Relative regional abundance of larvae of *Peprilus simillimus* according to CALCOFI collections, 1955–59: 3 = southern California; 4 = northern Baja California; 5 = upper central Baja California; 6 = lower central Baja California; 7 = southern Baja California. The number of larvae per 10 square meters of sea surface is an estimate calculated from standard haul totals. See Figures 39 and 41.

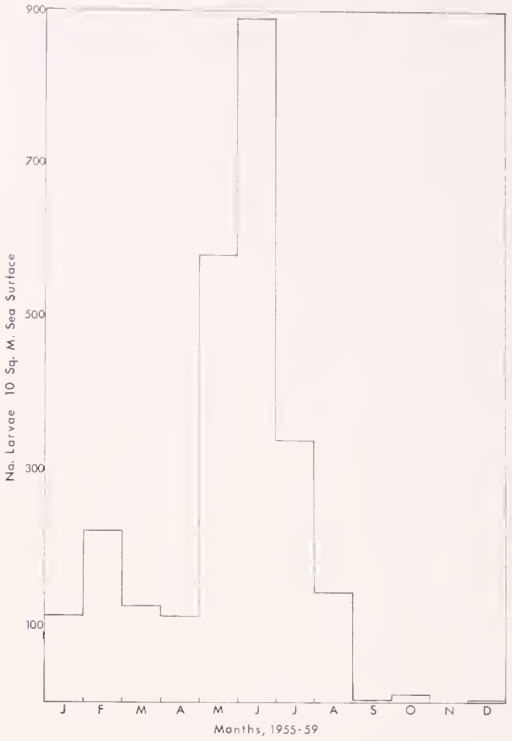


Figure 41. Cumulative monthly catch of larvae of *Peprilus simillimus* off the coasts of California and Baja California made by CALCOFI survey cruises, 1955–59. See Figures 39 and 40.

areas as Washington and British Columbia. The species remains to be of commercial importance only in California and mainly from Monterey to San Pedro.

Surface currents probably influence the extent of the northern distribution of *P. simillimus.* The data on the occurrence of this species in Washington and British Columbia are all similar in that the majority of captures are in the winter months, November through February, and that the size of the fish captured has been 150 mm FL or more. During the season of upwelling on the California coast (approximately March to July) a countercurrent (counter to the southward-flowing California Current) that contains considerable quantities of equatorial water flows close to the coast at depths below 200 m (Sverdrup, Johnson, and Fleming, 1942). In the fall upwelling ceases, and in the surface layers a countercurrent develops, the Davidson Current, which in November, December, and January flows northward along the coast to at least latitude 48°N. This latter current may particularly influence the movements of *P. simillimus.* Individuals may follow this current northward, and this may at least partially explain the captures of this species in northern areas in the winter months. In addition, the greatest numbers are landed commercially in California in the summer and fall with a decline in the catch in the winter and early spring (Fig. 43).

However, at least two factors cast some doubt on the proposal of a northward migration in winter and rather suggest the possibility of a resident, breeding population in the northern part of the range.

One factor is the gonadal condition of northern individuals. I have examined both male and female fish from Washington and British Columbia which had maturing and nearly mature gonads. These were fishes of 150 mm SL or larger. This is evidence for a northern spawning unless a southern migration occurs first. Eggs and larvae of this species have apparently not been found in northern waters.

A second factor which suggests a resident northern population is the apparent geographic variation which occurs in the length of the caudal fin. Individuals occurring from San Francisco to British Columbia have significantly shorter caudal fins than do those fishes taken from Monterey to Baja California (Fig. 14). Northern individuals also seem to have lower median fins than do southern forms. The importance of these variations is difficult to assess but it is suggestive of a distinct, resident population in the north, or at least of a clinal effect due to changing temperature conditions. The differences may only be between northern and southern California populations with those having the shorter caudal fin being resident off northern California and periodically migrating into more northerly waters.

While most northern occurrences have been in the winter months, *P. simillimus* has been collected at other times of the year. J. L. Hart (1949) reported that on 29 July 1946, about 150 pounds of this fish were taken in a bait seine in Bargain Harbor, British Columbia. Hart also quoted a crewman as saying that the species occurs throughout the year in British Columbia waters.

More information is needed in order to resolve the problems of breeding range versus geographic range and of seasonal migrations in *P. simillimus*.

P. paru, widely distributed in tropical, subtropical, and warm temperate waters in the Atlantic, is probably the most coastally-oriented fish of the genus. This species apparently does not migrate seasonally to offshore areas, but rather remains in relatively shallow water throughout the year (Table 22). H. H. Hildebrand (1954) caught *P. paru* during all months of the year on the shrimp grounds in the western Gulf of Mexico. Compton and Bradley (1963) reported that the fish was abundant in March at depths of 6 to 15 fms (11 to 27 m) in Texas coastal bays. J. M. Miller (1965) collected subadults in depths of 6 fms or less in the Gulf of Mexico near Port Aransas in February, March, and June. Copeland (1965) classed *P. paru* as a rare emigrant at Aransas Pass Inlet, Texas, and caught it in a tide trap in all seasons. I have collected mature and nearly mature individuals in the same tide trap during late June and early July. *P. paru* also appears to occur throughout the year in Chesapeake Bay on the Atlantic Coast.

P. burti occupies in the Gulf of Mexico a less extensive depth range than does *P. triacanthus* on the Atlantic Coast (Table 22). The species does, however, seasonally migrate to a limited extent.

Gunter (1945) collected *P. burti* in Aransas Bay, Texas, in March, August, and December; and in the Gulf of Mexico in March, April, May, June, and November. In Louisiana, the fish was taken most abundantly by Gunter in shallow areas in March. H. H. Hildebrand (1954) noted the presence of this fish on the shrimp grounds in the Gulf of Mexico throughout the year, but he stated that it was in greatest abundance in May and July, while during the winter it appeared sporadically and never in great abundance. Compton and Bradley (1963) found that it was one of the five most abundant fishes in Texas bay areas in March. They also stated that the fish breeds at a time of rising or high temperatures. According to J. M. Miller (1965), *P. burti* moves offshore with increasing water temperatures in the spring. Copeland (1965) listed this species as an occasional emigrant at Port Aransas Inlet, Texas, taking it in tide trap collections

from November through May and most abundantly in April. The pattern seems to be that individuals are in shallow inlets and bays during the winter and early spring; then as the water temperature increases, the fish move offshore into the Gulf, yet not into much deeper water. Spawning probably occurs offshore in the surface layers of the Gulf during late spring, summer, and perhaps early fall.

The seasonal movements of *P. burti* seem to correlate with the temperate affinities of the species. The movements are the reverse of that of its close relative, *P. triacanthus*, but similar in that both remain in temperate waters. *P. burti* avoids subtropical temperatures, and *P. triacanthus* migrates to avoid boreal temperatures in the northern part of its range.

Little information is available on the other three species. *P. ovatus* is a shallow-water species of restricted distribution in the northern Gulf of California and probably does not migrate seasonally. The species has been collected at depths of 45 m or less. *P. medius* is often collected in shallow water, including bays and inlets and in depths of 90 m or less. This species probably migrates seasonally only to a limited extent. *P. snyderi* has been collected in inshore areas; however, its rareness in collections suggests that it may periodically inhabit deep water.

Faunal associations. At a size of about 10 to 30 mm SL, a portion at least of the populations of the species of *Peprilus* becomes associated with scyphomedusae and siphonophores (hereafter, both referred to as jellyfish medusae). This association may continue until the fish reach a size of 100 mm SL. The relationship is a widely recognized and well-documented one. Mansueti (1963) has reviewed the literature of the subject and has provided new data on the symbiotic behavior between *P. paru* and the jellyfish, *Chrysaora quinquecirrha*. The association is widespread among the stromateoid fishes according to Haedrich (1967). The relationship also occurs in the Carangidae, a pelagic family, in the Gadidae, Girellidae, and Centriscidae, all demersal families, and in the Zaproridae, an abyssal family (Mansueti, 1963).

The importance of the association in the life of these fishes is not well understood. The young fish may gain several advantages from the relationship including protection from predators, a source of food (the jellyfish itself), a concentration of food resulting from presence of small invertebrates among the tentacles and under the bell of the jellyfish, a means of dispersal, and possibly a means of reducing interspecific competition. Walford (1958) stated that jellyfish are among the most valuable animals in the sea in that they give shelter to the young of a number of species of fishes. He added that the small fish travel with their host in the plankton, feeding around it within a radius of a few feet, darting to safety beneath the umbrella when threatened by enemies. The fish continue this mode of life as long as it is advantageous to them, e.g., until they are ready to become independent. Walford suggests that this association may be an essential stage in the life cycle of some fishes.

At least in the stromateid fishes, and particularly in *Peprilus*, the association may not be obligatory. I have collected two species of *Peprilus*, *P. burti* and *P. paru*, which were not with jellyfish, as have others for *P. triacanthus* and *P. paru* (Bigelow and Schroeder, 1953; Mansueti, 1963). Mansueti classifies the association as a temporary ecological phenomenon resulting from a series of extrinsic chance factors in which jellyfishes are the passive hosts and fishes the active opportunists. *P. paru* begins a commensal association by consuming plankton and other organisms found on or near the hosts and then gradually becomes parasitic as it feeds on parts of the medusa. Finally, in autumn, as a large non-symbiont, it becomes predatory upon the medusae. Cargo and Schultz (1966) stated that schools of *P. paru* larger

than 50 mm in length may destroy large numbers of scyphozoan medusae in minutes.

The fish itself is apparently rarely killed or eaten by the medusae. According to Mansueti (1963), the nature of the symbioses suggests that most associated fishes have some immunity to jellyfish toxin, and that either the immunity is gradually acquired through gradual adaptation, or that some or all fish symbionts may possess natural antibodies. A protective agent may be present in the mucous secreted by symbiotic fish which may either inhibit nematocyst discharge or counteract the toxin after stinging occurs. Species of *Peprilus* do secrete considerable amounts of mucous, and the extensive canal system may be involved in achieving immunity as suggested by Miner (1936).

The temporary association between *Peprilus* and jellyfish may be discontinued because of several factors: rapid growth of the fish and feeding independently from the jellyfish; the physical size attained by the fish; seasonal changes in hydrographic conditions – cold water temperatures in late autumn resulting in the death of certain jellyfish such as *Chrysaora* in Chesapeake Bay (Mansueti, 1963); or, similar to the first factor, a change in food habits of the fish, such as feeding in deeper waters.

The association does not involve the entire population of the fish species, which is to be expected since it is considered to be a fortuitous relationship. Stromateid fishes are known to be nonsymbiotic at the same size and in the same months as symbiotic stromateid fishes. The contacts between fish and jellyfish may be explained by the random search of the fishes for concentrations of food with such movement bringing the two organisms into close association. The coincidence of a period of pelagic existence among the young fish in the same area of a high incidence of pelagic jellyfishes seems important in developing the association.

The association is not species-specific, at least in *P. paru, P. triacanthus,* and *P. burti. P. paru* is known to consort with five jellyfish genera, *Chrysaora, Chiropsalmus, Cyanea, Aurelia,* and *Physalia* (a siphonophore). *P. triacanthus* has been found with *Chrysaora, Cyanea, Stomolophus,* and *Physalia. P. burti* in the Gulf of Mexico is known to associate with *Stomolophus meleagris* and *Aurelia* sp. Specimens of *P. simillimus* of about 30 to 50 mm in length have been found with *Pelagia* (SIO H52–221 and 60–409). This information suggests that the association is a loose one and gives additional support to the theory that the relationship is largely a fortuitous one and not geared to a species-specific, obligatory condition. The association is unique in the sense that the symbiont is not physically attached to the host (jellyfish) but is free in the immediate vicinity. This may account for the looseness of the relationship and increases the difficulty of attempting to categorize the association.

The young of many pelagic fishes gather under a variety of animate and inanimate floating objects at sea. The objects may be seaweed, large living animals, driftwood, or rafts of various origins. Gooding and Magnuson (1967) refer to the floating object in the pelagic environment as being a relatively rare "superstrate" in an environment notable for its horizontal homogeneity. This superstrate, they suggest, has some of the same ecological significance to certain pelagic fishes that a substrate has to inshore fishes. They cite shelter from predation as probably the most significant factor in the evolution of fish communities that gather beneath inanimate drifting material in the open ocean. The fish-jellyfish association seems to be different in that it persists where the inanimate relationship may terminate (Mansueti, 1963). The fish-jellyfish relationship, even though temporary itself, seems to be of a more sustaining nature in that the host provides shelter, protection, and food.

If precise categorization and a more

Table 23. List of the Ten Fish Species Seasonally Collected Most Regularly and Abundantly with the Butterfish, *Peprilus triacanthus*, by R/V ALBATROSS IV Groundfish Survey Cruises (U. S. Bureau of Commercial Fisheries, Woods Hole, Mass.) off the Northeastern Coast of the United States for the Years 1963 through 1966.

Species	Summer (Jul–Aug)	Autumn (Oct–Nov–Dec)	Winter (Jan–Feb)
Spiny dogfish (*Squalus acanthias*)*	×	×	×
Little skate (*Raja erinacea*)*	×	×	
Haddock (*Melanogrammus aeglefinus*)	×	×	
Silver hake (*Merluccius bilinearis*)*	×	×	×
Squirrel hake (*Urophycis chuss*)*	×	×	×
Alewife (*Alosa pseudoharengus*)	×		
Yellowtail flounder (*Limanda ferruginea*)	×	×	
Winter flounder (*Pseudopleuronectes americanus*)		×	
Fourspot flounder (*Paralichthys oblongus*)		×	×
Longhorn sculpin (*Myoxocephalus octodecimspinosus*)		×	

* Butterfish known to be a part of diet.

complete understanding of the fish-jellyfish association are to be achieved, underwater observations in the natural environment and further careful laboratory studies are necessary.

Table 23 is a list of the species of fishes which were collected in greatest abundance with *P. triacanthus* over a three-year period during three seasons, summer, autumn, winter, off the northeastern coast of the United States (Fig. 37) by groundfish surveys of the Bureau of Commercial Fisheries, Woods Hole, Massachusetts. A number of the species are large carnivores and feed on small fishes. Some of them are known to prey on *P. triacanthus*, and probably all the species listed in Table 23 occasionally feed on this species. The importance of *P. triacanthus* as a forage species becomes especially evident since it probably forms a substantial portion of the diet of such commercially valuable species as haddock, silver hake, and squirrel hake.

The season of the year that certain of the species listed in Table 23 occur or are collected most abundantly with *P. triacanthus* reflects the habits and temperature affinities of these species as compared with the same characteristics of *P. triacanthus*. The haddock (*Melanogrammus aeglefinus*) is a boreal species inhabiting cool waters, particularly north of Cape Cod (41°N) (Fritz, 1965). *P. triacanthus* occurs north of Cape Cod only in the summer and early autumn when temperatures are warmer; hence, the two species are collected together only in summer and autumn. Yellowtail (*Limanda ferruginea*) are also collected with *P. triacanthus* mainly in the summer and autumn. The former species is apparently confined to shoal waters (Bigelow and Schroeder, 1953) which *P. triacanthus* abandons during the winter for deeper water. The longhorn sculpin (*Myoxocephalus octodecimspinosus*) is a winter spawner, probably in shallow, coastal waters (Bigelow and Schroeder, 1953), which would explain its absence in areas of concentrations of *P. triacanthus* in the winter. The little skate (*Raja erinacea*) and the winter flounder (*Pseudopleuronectes americanus*) are bottom fishes with a depth range extending only to about 136 m (Bigelow and Schroeder, 1953), which would tend to explain why both species are taken with *P. triacanthus* only in the summer and autumn. Three species, silver hake (*Merluccius bilinearis*), squirrel hake (*Urophycis chuss*), and spiny dogfish (*Squalus acanthias*), range widely both north and south of Cape Cod at various depths (Fritz, 1965), and, accord-

ingly, the three are captured in abundance in all three seasons with *P. triacanthus*.

General food habits. Stomach contents of the fishes of this genus are often very difficult to identify. The type of material making up a portion of the diet and the shredding action of the teeth of the pharyngeal sac frequently result in stomachs containing chunks of whitish or transparent, amorphous tissue. No attempt has been made to present a quantitative account of food habits of any species. Rather, a general summary is given of the results of examination of food items which I have made in three species of *Peprilus* and of reports in the literature of food studies in this genus and in the related genus *Pampus*.

The teeth, mouth size, and digestive tract are very similar among all the species of *Peprilus*. Food habits and feeding behavior are probably similar in all species of this genus. Differences which do exist may be quite subtle and might result from shifts in diet with age, from an increase in size associated with a shift in mode of life, from seasonal availability of certain food items, or from niche separation and character displacement in sympatric situations. The latter possibility deserves investigation.

The species of *Peprilus* consume a variety of food items. Bigelow and Schroeder (1953) stated that *P. triacanthus* in the Gulf of Maine feeds on small fish, squid, crustaceans such as shrimp and amphipods, annelid worms, and to a lesser extent, ctenophores. Haedrich (1967) reported that the shredded transparent tissues which predominated in the stomachs he examined were probably jellyfish, ctenophores, and salps. I have examined the stomach contents of freshly captured specimens of three species, *P. triacanthus*, *P. burti*, and *P. paru*. In one group of specimens of *P. triacanthus* ranging in size from 24 to 41 mm SL, the stomachs were generally full of chunks of whitish material which was identified as parts of jellyfish, especially the tentacles. Jellyfish remains constituted the bulk of the stomach contents of 20 specimens of *P. burti* ranging in size from 55 to 100 mm SL. Crustaceans including small amphipods, shrimp, and zoea larvae, and postlarval fish were also present in the stomachs of these fish. The stomachs of a few large (up to 150 mm SL) specimens of *P. paru* contained jellyfish remains and small crustaceans.

The association of young *Peprilus* with jellyfish medusae seems to be correlated with the feeding habits of the fish. That the young fish feed on their jellyfish hosts has been reported on several occasions (Miner, 1936; Mansueti, 1963; Cargo and Schultz, 1966; and others). Mansueti made monthly collections of symbiotic *P. paru* and found that the stomachs of these fish invariably contained masses of whitish, coagulated material which he identified as parts of scyphomedusae. A small amount of other food items, mainly small invertebrate remains, were also found in the stomachs of these fish which ranged in size from 21 to 80 mm TL. Stomachs of small, nonsymbiotic *P. paru* examined by Mansueti also contained masses of coagulated medusan tissue, some small invertebrates, and other material, largely unidentifiable. The young fish considered to be nonsymbiotic may actually be symbiotic except that they were away from the host when captured. The association is admittedly a loose one.

Although medusae are usually considered to be low in nutrients and high in water content per unit volume, young *Peprilus* seems certain to derive some nourishment from the protein structure of jellyfish. Mansueti (1963) found that in aquaria, *P. paru*, satiated and markedly distended from voracious feeding on *Chrysaora*, rapidly lost the distension suggesting the efficient utilization of jellyfish tissue and absorption of the liquid contents. Jellyfishes may be an important source of protein for young fishes during the critical early stages of growth in the summer and autumn.

Changes in the feeding and other behavioral patterns appear to occur in young

Peprilus by late autumn. Autumn seems to be the period when the symbiotic relationship dissolves, at least in Atlantic coastal waters, particularly around Chesapeake Bay. This separation may be followed by a short period of voracious feeding upon scyphomedusae and ctenophores (Dunnington and Mansueti, 1955; Cargo and Schultz, 1966). The end of the association often correlates with a loss in hosts, especially of *Chrysaora* which undergoes mass mortalities with a drop in water temperatures in late October and early November (Mansueti, 1963).

The pattern seems to consist of feeding largely upon jellyfish until a size of about 100 mm SL is reached. The association ends as the fish increase in size and hydrographic conditions change. This is followed by continued feeding upon jellyfish but to a lesser extent. The diet then consists of proportionately more crustaceans, worms, squid, and small fish.

Suyehiro (1942) reported that another stromateid fish, *Pampus argenteus,* feeds principally on jellyfish in Japanese waters, although his conclusion was based on limited data. Nath (1966) in a study of the fishes off the Travancore coast of India found that *Pampus argenteus* was a macroplankton feeder and that the variation in diet of the species depended largely upon the seasonal changes in abundance of crustaceans and polychaetes. From November through March amphipods and copepods are abundant, and during this period these crustaceans predominated in the stomachs of *Pampus argenteus.* In April, the diet consisted almost entirely of crustaceans. By June, the crustaceans declined and were replaced in the diet by polychaete worms until September. Nath did not find medusae in the stomachs of this species. Kuthalingam (1963) found results similar to those of Nath with the same species in the Bay of Bengal. He reported that young *Pampus argenteus* ate primarily copepods and other small crustaceans, while the adult fish are principally a variety of small crustaceans, as well as larger crustaceans, polychaetes, and small fish. Menon (1942) stated that larger specimens of *Pampus chinensis* off the Trivandrum coast of India feed on fishes, mainly anchovies, and younger ones on crustaceans and polychaetes.

The above data on *Pampus* indicates that the food and feeding habits of these fishes depend upon such factors as size and growth rate of the fish, seasonal and local abundance of food organisms, and the type and length of symbiotic relationships.

Commercial importance. Some of the species of all three genera of stromateid fishes are of commercial value. The fishes are oily and all species which are used commercially are said to be of delicate texture and fine flavor. *Pampus* is the most important genus commercially of the suborder Stromateoidei. Species of *Pampus* are important food fishes along the coasts of India, China, and Japan, being much in demand and bringing a high price in most areas. Species of *Stromateus* support only local fisheries along the coasts of west Africa, Chile, Argentina, and Uruguay. The potential fishery value of the species along the coasts of the latter two countries is probably much greater than generally suspected (T. J. Hart, 1946). Three species of *Peprilus, P. triacanthus, P. simillimus,* and *P. paru* are of considerable commercial value, although the catch of each species is subject to large yearly fluctuations, and none of the species forms a major part of the fishery in their respective regions. *P. triacanthus* forms the largest fishery among the fishes of the genus.

P. triacanthus, commonly known as the "butterfish" in fisheries literature, is mainly of importance along the coasts of the northeastern and middle Atlantic states. Its fishery has been discussed by Hildebrand and Schroeder (1927) for the Chesapeake Bay region and by Bigelow and Schroeder (1953) for the Gulf of Maine. This species is landed in recordable amounts from Maine to North Carolina,

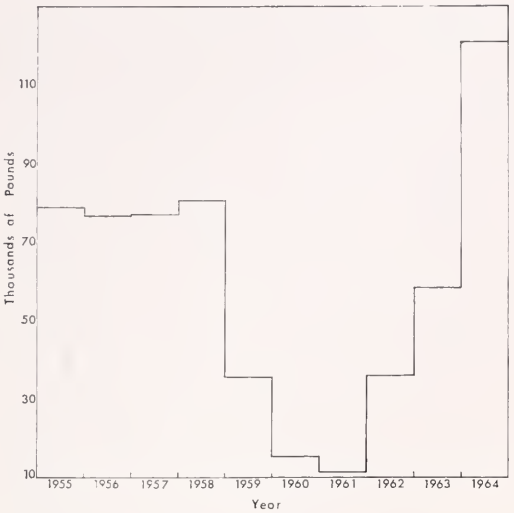


Figure 42. Yearly commercial catch of *Peprilus simillimus* off the coast of California, 1955–64. Data compiled from Staff, Marine Resources Operations (1958), Biostatistical Section, Marine Resources Operations (1960a, 1960b, 1961, 1963, 1964, 1965), and Greenhood and Mackett (1965).

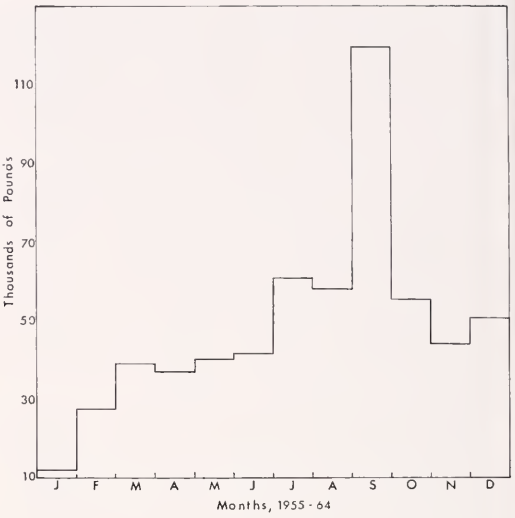


Figure 43. Cumulative monthly commercial catch of *Peprilus simillimus* off the coast of California, 1955–64. Source of data same as for Figure 42.

and the largest landings are in Rhode Island, New Jersey, New York, Massachusetts, and Virginia (Power, 1962; Lyles, 1966). The species is not of importance south of North Carolina even though its range extends to southern Florida. In Massachusetts, it is available in fresh fish markets throughout most of the year and is usually sold at a weight of about one-fifth to one-half pound and a length of six to nine inches. It is usually captured by otter trawl, haul seines, or pound nets. In the Chesapeake Bay region, about equal quantities are taken in the Bay proper and in oceanic areas. The characteristics of small body cavity, relatively soft bones, and high muscle content combined with its habit of forming large concentrations in winter in deep water may indicate that this species is of considerable potential value for use in the manufacture of protein supplements and fishmeal.

P. paru, the "harvestfish" of fisheries literature, is of important commercial value only on the Atlantic Coast of the United States despite its much wider distribution in the Atlantic. This species is landed in largest amounts in the Chesapeake Bay region mainly off Virginia and North Carolina. It was not recorded in the commercial catch either north of Virginia or south of North Carolina in 1960 and 1964 (Power, 1962; Lyles, 1966). *P. paru* is not sold in the Gulf of Mexico in any recordable numbers although it occurs throughout the region in considerable abundance. Baughman (1941) has stated that this fish does not reach sufficient size in Texas to be of economic value. The size difference seems to be slight, however. Small local fisheries may exist for this fish southward to Brazil. In the Chesapeake Bay region almost twice the poundage is landed in the Bay proper compared to the adjacent oceanic areas (Lyles, 1966). This demonstrates somewhat the inshore nature of this species compared to *P. triacanthus* which in the same region is caught in about equal amounts in the Bay proper and in oceanic areas.

P. simillimus, the "Pacific pompano" or just "pompano" of Pacific fisheries litera-

ture, has a wide distribution (British Columbia to southern Baja California), but is of commercial value only in the southern half of California from Monterey to San Diego. The biggest landings by far are in San Pedro and Monterey, California (Power, 1962; Lyles, 1966). The annual and monthly catches of this species fluctuate widely (Figs. 42 and 43) according to data compiled from Staff, Marine Resources Operations (1958), Biostatistical Section, Marine Resources Operations (1960a, 1960b, 1961, 1963, 1964, and 1965), and Greenhood and Mackett (1965). Largest monthly landings occur in the summer and early autumn. *P. simillimus* is a minor species in terms of the total catch; but with its rich flavor and flaky texture, it is considered a delicacy and brings a high price. It is sold entirely in fresh fish markets. The major portion of the catch is taken in lampara nets and purse seines, and a fair quantity is taken on hook-and-line by pier fishermen.

P. burti of the Gulf of Mexico apparently does not attain the size of its close relative, *P. triacanthus*, on the Atlantic Coast. As already mentioned, *P. paru* in the Gulf of Mexico is reported to not reach the size of members of populations of the same species on the Atlantic Coast. These two situations may illustrate the trend observed by Lindsey (1966) that fishes tend to be larger in higher latitudes. *P. burti* is of little or no commercial importance in the Gulf of Mexico. According to Gunter (1945), few members of this species reach large size in Texas waters and they are never sold for food there. H. H. Hildebrand (1954), who caught large numbers of this species on the Texas shrimp grounds, reported that the largest specimen caught measured 173 mm (SL or FL?). Gunter (1945) caught one specimen which measured 200 mm (SL or FL?) which may be nearly maximum size. *P. triacanthus* may reach a length of 300 mm FL.

No information is available on the economic status of *P. ovatus* in the northern Gulf of California, but, because of its apparently small size and restricted distribution, it is probably of little or no commercial importance.

The extent of the commercial value of *P. medius* and *P. snyderi* is uncertain although both species do appear in fish markets along the coasts of Mexico and Central America. Each species probably constitutes a minor element of the fishery in these regions.

EVOLUTIONARY RELATIONSHIPS AND ZOOGEOGRAPHY

A number of attributes of the stromateid fishes and of the genus *Peprilus* in particular invite study into the relationships and zoogeography of the group. The genus *Peprilus* is a member of an advanced family and has a widespread, continuous distribution along the coasts of the New World. Some of the species are widely distributed, two are more restricted, and all are confined to the continental shelf. None of the species cross oceanic barriers. *Peprilus* is largely allopatric with the other stromateid genera, and it is possible to correlate tectonic activity of recent epochs with the present distributional pattern of the members of the genus.

Origin of the genus Peprilus and its position among stromateoid fishes. Certain evidence suggests a Tethyan distribution for early members of the family Stromateidae or its ancestors. These fishes, though low in the number of species, were probably widely distributed in shallow coastal areas of the large Tethys Sea which in the early Tertiary combined the Indo-West Pacific, the Mediterranean, the tropical Atlantic, and the East Pacific faunas into one major unit (Ekman, 1953).

The first tectonic activity in the western Tethys which led to eventual isolation of the Mediterranean probably occurred in the early Tertiary (Fell, 1967). The disruption of the Tethys by emergence of

land areas began in the Oligocene and was well developed in the Miocene (Kummel, 1961). From that time on the Indo-West Pacific realm was isolated from the western end of the Tethys Sea, and the Mediterranean Sea was formed.

The events described above may have divided and isolated segments of the ancestral stromateid fishes. *Pampus* probably evolved in isolation from other stromateids in the eastern Tethyan region. The ancestral stromateid stock in the western Tethyan region probably gave rise to *Stromateus* and *Peprilus*. *Stromateus* probably emerged in the Mediterranean and West African region, and in at least partial isolation, *Peprilus* probably evolved in the American region. The divergence of the evolutionary lines leading to *Stromateus* and *Peprilus* had possibly begun before the division of the Tethys Sea since Fell (1967) has indicated that passage and exchange of faunal elements through the western Tethyan region had become increasingly difficult before the Miocene.

Stromateus occurs along the southern coasts of South America and is the only stromateid to occur on both sides of an ocean. However, its transoceanic dispersal is across the shortest possible route, the South Atlantic. *Stromateus* of southern South America is similar to *Peprilus snyderi* of the eastern tropical Pacific. The two genera may share a common ancestor in the western end of the Tethyan element. *Stromateus* of South America has retained its generic affinities with *Stromateus* of Africa, but approaches *Peprilus* in several characteristics including: a reduced number of precaudal vertebrae; two epural elements in the caudal skeleton (three in the African *Stromateus*); and no pelvic fins in the young (see Haedrich, 1967: 102). Its systematic position seems to be somewhat intermediate between *Stromateus fiatola* of Africa and *Peprilus snyderi*. It may be more closely related to *Peprilus*, but further study is needed.

There was a direct connection between the Atlantic and Pacific Oceans before the formation of the Central American land bridge in the Pliocene, and there were probably few or no serious obstacles to widespread distributions of shallow, warm-water, marine organisms. The cooling of the climates which began in the middle and late Cenozoic and culminated in the Pleistocene glaciations (Kummel, 1961) apparently had not progressed by this time (lower Pliocene) so as to be a strongly limiting force to the distribution of tropical faunas. C. L. Hubbs (1960) has attributed in considerable part the low generic endemism in the Panamic fauna to the fact that this fauna is largely a part of the common Atlantic-Pacific tropical fauna of the New World. Hence, the stock of *Peprilus* was probably rather wide-ranging in an Atlantic-Pacific province of warm water. The distribution probably extended into what would be today temperate latitudes on the Atlantic and Pacific coasts. Few barriers existed to segregate populations, and speciation was probably at a low level.

North and South America became connected by an isthmus in the Pliocene (Schuchert, 1935; Lloyd, 1963; Simpson, 1950), and since that time, the Atlantic and Pacific faunas have evolved separately. The genus *Peprilus* has been divided geographically for several million years, depending upon the time of complete emergence of the isthmus and the duration of the Pliocene and the Pleistocene. After this separation, the cooling of the climates, the alternating effects of the Pleistocene glacial and interglacial periods, the resultant emergence and submergence of land barriers, and the establishment of persistent tropical-temperate conditions have provided the barriers for isolation and the resulting speciation in the genus.

Despite the basic morphological similarity among members of the genus, differences are apparent in body proportions, meristic values, premaxillary teeth, in the length of the anterior lobes of the median

fins, and in the presence and size of body pores. Two somewhat subtle species groups, or at least two separate trends, exist within the genus. One group consists of relatively elongate fishes with low median fins; the species in this group are *P. snyderi*, *P. simillimus*, *P. triacanthus*, and *P. burti*. The second group exemplifies the trend toward a deep body and falcate median fins and is composed of *P. paru*, *P. medius*, and *P. ovatus*. Both trends or species groups apparently were established before the closing of the Central American seaway since each group is represented in both the Atlantic and Pacific oceans. Rosenblatt (1963) likewise has found that the two species groups of the tripterygiid genus *Enneanectes* are each represented in both oceans.

Primitive and derived conditions. Without fossil material, it is difficult and somewhat conjectural to attempt to determine which taxa within a group are primitive and which are derived. However, the situation becomes more approachable when a larger group containing the one in question can be placed in a reasonable evolutionary perspective. Haedrich (1967), largely on the basis of osteological evidence, has provided a concept of the evolutionary trends in the suborder Stromateoidei. Haedrich places the family Stromateidae at the zenith of stromateoid evolution and considers the ancestor of the family to be among the hard-spined members of the family Centrolophidae, probably a fish similar to the genus *Psenopsis*. Members of this genus are small (up to 200 mm SL), elongate, with small mouths, deciduous scales, the dorsal fin with only slightly more rays than the anal fin, and a vertebral number of 10+15.

I consider *P. snyderi* (Fig. 16) to be the most primitive species of *Peprilus* and most nearly like the ancestral form which gave rise to *Stromateus* and *Peprilus*, and probably *Pampus* as well. Compared to *Psenopsis*, all stromateids have an increased number of vertebrae and median fin-rays. *Pampus* and *Peprilus*, the latter especially, have lower meristic values than *Stromateus*, and Haedrich (1967) considers *Pampus* to be the most advanced stromateid genus. The ancestral or early stromateid forms probably had an increased number of vertebrae and median fin-rays relative to the centrolophid form from which they evolved. I therefore consider the high number of vertebrae and other meristics of *P. snyderi* to represent the primitive condition in the genus, and the reduced number to be the derived condition. *P. paru* (Fig. 24) is considered to be the most highly derived species, although no suggestion is made that this species is the most recently evolved. The divergence began early in the history of the group, before separation by the Central American land bridge, and has continued to the present. *P. paru*, with its very deep body and extremely falcate dorsal and anal fins, has diverged further from the presumed ancestral condition than any other member of the genus. *Pampus* has in several respects paralleled the evolutionary direction taken by *P. paru*.

A fairly strong continuum of types exists between the primitive type, *P. snyderi*, and the derived type, *P. paru*. This range of forms strongly supports the concept that this group of species constitutes a single genus rather than the three (including *Palometa* and *Poronotus*) in common usage. Although *P. paru* differs in several respects from *P. snyderi* and the other elongate species, its affinities with these species are strong. The group fits well into the category genus as defined by Mayr, Linsley, and Usinger (1953).

There does exist in *P. triacanthus* and *P. burti* the possible beginnings of another divergence or evolutionary direction. These two species have a row of relatively large pores of varying number and regularity below the dorsal fin (Figs. 19 and 21–22), and also have cusped rather than pointed or simple premaxillary teeth (Fig. 33b). The function of either attribute is unknown

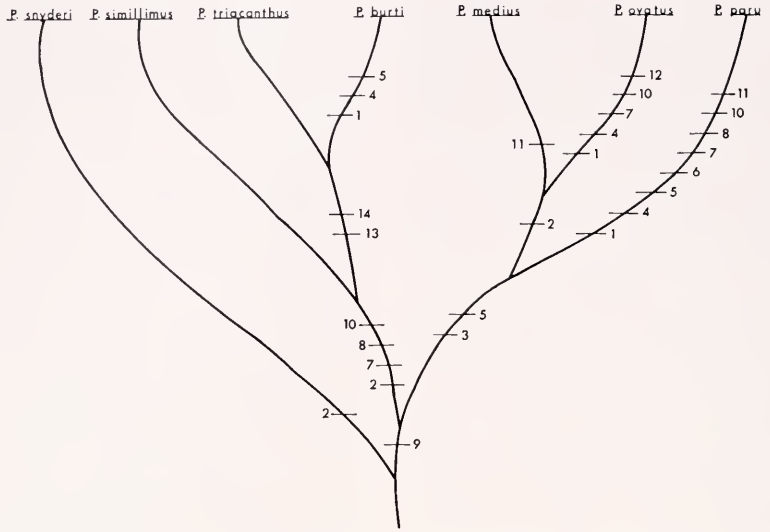


Figure 44. Dendragram of probable species relationships in the genus *Peprilus*. The evolutionary steps which increase character-state codes for each character are shown as lines across the branches. The number of the character represented is next to the horizontal line and corresponds to one of the list of characters in Tables 24 and 25. Explanation in text.

and neither seems to represent as yet a major evolutionary shift. The presence of the row of pores has been used as a generic character; however, it does not appear to be specially innervated, but rather to be a slight elaboration of the subdermal canal system which is present in all the members of the genus. *P. ovatus* (Fig. 10) frequently has a series of medium-sized, irregularly-spaced pores along the dorsal surface of the body, a somewhat intermediate condition. Regarding the premaxillary teeth, two other members of the elongate species group, *P. snyderi* and *P. simillimus*, generally have pointed premaxillary teeth, but a particular specimen of either species may have a few teeth with two or three small cusps, an intermediate condition. In other aspects of morphology and ecology *P. triacanthus* and *P. burti* have strong affinities with the other members of the genus.

As Cain (1956) has stated, the genus is not necessarily definable by one peculiar attribute, nor are its constituents monotypic, equivalent, essentially merely subdivisions of it, or themselves wholly discrete. Inclusion of the seven stromateid species within a single genus appears to be a natural and instructive classification consistent with the evolutionary, morphological, and distributional characteristics of the members.

Intrageneric relationships. A dendrogram of species relationships in the genus *Peprilus* is presented in Figure 44. The dendrogram fits the definition given by Mayr, Linsley, and Usinger (1953) and the definition of a cladogram given by Camin and Sokal (1965). A time scale or a phylogeny is not inferred.

Several methods have recently been published (Edwards and Cavalli-Sforza, 1964; Camin and Sokal, 1965; Wilson, 1965) concerning the reconstruction of cladistic relationships based on the characters of contemporaneous species. In reconstructing the dendrogram of Figure 44, I have used the quantitative method of Camin and Sokal in association with con-

Table 24. Characters and Character States Applied to Dendrogram of Species Relationships in *Peprilus*. Mean morphometric values in thousands of SL. See Table 25 and Figure 44.

Character	Character-State Codes 0	1	2
1. Eye diameter	$\bar{x}$ 070–086	093–103	
2. Interorbital width	$\bar{x}$ 087–097	112	
3. Pectoral fin length	$\bar{x}$ 312–336	360–386	
4. Preanal distance	$\bar{x}$ 424–445	465–484	
5. Body depth	$\bar{x}$ 427–461	529–619	710
6. Caudal peduncle depth	$\bar{x}$ 065–079	092	
7. Mean dorsal ray number	46.5–46.7	42.8–44.8	
8. Mean anal ray number	42.0–43.9	39.5–40.4	
9. Precaudal vertebrae	14–15	13	
10. Caudal vertebrae	20–22	16–19	
11. Anterior lobes of median fins	$<$ 6 times length of shortest ray	$\geq$ 6 times length of shortest ray	
12. Ratio of dorsal rays to anal rays	> 1.0	$= 1.0$	
13. Row of dorsal pores	absent	present	
14. Premaxillary teeth	simple	cusped	

ventional methods. The distribution of the species and the probable position of the genus in the suborder have been important in establishing the species relationships. The reasons for using the Camin-Sokal method are mainly for systematization and quantification and for increased objectivity. The method, although not greatly different from conventional methods, allows the procedure of reconstruction to be more easily followed.

The Camin-Sokal method requires several assumptions to be made: that characters be expressed in discrete states differing among at least some of the species; that characters can be arrayed in some logical order; that there is a knowledge of evolutionary trends so the characters can be arrayed in a presumed evolutionary sequence from primitive to derived; that the ancestral state arose only once in the taxa, although derived character states may have arisen repeatedly in different branches; and, that evolution is irreversible for each character state. The most parsimonious cladogram is considered to be the most plausible one. Primitive character states are coded as zero, derived states positively or negatively as required (Tables 24 and 25).

Table 25. Data Matrix of Character-State Codes for the Species of *Peprilus*. See Table 24 and Figure 44. Explanation in text.

Character	*snyderi*	*simillimus*	*triacanthus*	*burti*	*medius*	*ovatus*	*paru*
1. Eye diameter	0	0	0	1	0	1	1
2. Interorbital width	1	1	1	1	1	1	0
3. Pectoral fin length	0	0	0	0	1	1	1
4. Preanal distance	0	0	0	1	0	1	1
5. Body depth	0	0	0	1	1	1	2
6. Caudal peduncle depth	0	0	0	0	0	0	1
7. Mean dorsal ray number	0	1	1	1	0	1	1
8. Mean anal ray number	0	1	1	1	0	0	1
9. Precaudal vertebrae	0	1	1	1	1	1	1
10. Caudal vertebrae	0	1	1	1	0	1	1
11. Anterior lobes of median fins	0	0	0	0	1	0	1
12. Ratio of dorsal rays to anal rays	0	0	0	0	0	1	0
13. Row of dorsal pores	0	0	1	1	0	0	0
14. Premaxillary teeth	0	0	1	1	0	0	0

I began reconstruction of the cladogram using a total of 31 characters. Some of these could not be coded with any certainty or showed no differences among the species and thus provided no additional information. As a result, 14 characters were applied to the cladogram. These are presented in a data matrix with the appropriate character-state codes for each of the 14 characters (Table 25). The character states with the assigned character-state codes are listed in Table 24.

The primitive and derived character states were determined by examining the members of the genus in the perspective of the entire suborder. Certain character states correspond to apparent trends existing in the genus and represent conditions different from, or advanced relative to, the basal or primitive character states of some members of the genus or the presumed ancestral types of the suborder. The character states considered to be derived include: an increased eye diameter; a greater interorbital width; a longer pectoral fin; a greater preanal distance; increased body and caudal peduncle depths; and, lower numbers of dorsal and anal rays and of caudal and precaudal vertebrae (see Table 24 and the preceding discussion of primitive and derived conditions). The elongate lobes of the median fins, the approximate one-to-one ratio of dorsal and anal rays, the presence of a row of dorsal pores, and the cusped premaxillary teeth (characters 11, 12, 13, and 14; Table 24), are considered to be derived character states and were easier to code than the above states because they are discrete and unique to certain species in the sense of being present or absent.

The cladogram was reconstructed by the monothetic method described by Camin and Sokal. Evolutionary steps increasing character-state codes are shown graphically as short lines across the branches (Fig. 44). The number of the character represented by a short line is listed next to that line. It was necessary to test for parsimony and to make adjustments. The final cladogram requires 28 steps and is parsimonious in the context of information available.

The Camin-Sokal method was of use in determining the relationships of a newly described species, *P. ovatus*. The cladogram supports the assumption of a close relationship between *P. ovatus* and *P. medius*.

P. snyderi has the assumed primitive condition of all but one of the characters used in the reconstruction of the cladogram. The line leading to *P. simillimus*, *P. triacanthus*, and *P. burti* developed before the formation of the Central American land bridge. *P. burti* and *P. triacanthus* are seen as recently diverged species; *P. burti* has attained some advanced character states including a deeper body, a larger eye, and fewer vertebrae. The *paru-medius* line was probably divided by formation of the Central American land bridge. The high number of changes in character states for *P. paru* is illustrated in the cladogram and indicates the derived condition. *P. ovatus* secondarily approaches *P. paru* in a number of aspects including the short, deep body, the large eye, and the reduced number of vertebrae.

Parallelism and species pairs. As mentioned above, *P. triacanthus* of the Atlantic and *P. simillimus* of the Pacific closely resemble one another. Both are moderately elongate fishes with low dorsal and anal fins (Figs. 13 and 21). These two species show the closest similarity of any two in the genus in the summed differences of certain morphometric and meristic characters (Table 26). Their respective distributions complement one another on opposite coasts. Both reach their northern distributional limits at about 48°N, *P. triacanthus* as an occasional visitor on the southern coast of Newfoundland, and *P. simillimus* as an element in low abundance in coastal waters of southern British Columbia. The southern limits of their distributions are also similar. *P. triacanthus*

ranges to about 27°N off the coast of southern Florida, with likely infrequent occurrences in the Gulf of Mexico; one record exists for the southeastern Gulf of Mexico (UW 13407). *P. simillimus* occurs as far south as about 24°30′N in Bahía Magdalena, Baja California; one specimen is known from the Gulf of California, in Bahía Los Angeles (SIO 62–236). Each species migrates seasonally in at least part of its geographic range.

P. triacanthus is of greatest abundance in the northern part of its range, North Carolina to the Gulf of Maine, as is attested by its relative abundance in the commercial landings in this region. *P. simillimus* is of most common occurrence in the southern part of its distribution, chiefly from San Francisco to Baja California. It is caught commercially only from Monterey to San Diego in California. Catches of the species in Washington and British Columbia are small and sporadic. The major surface currents, the Gulf Stream in the Atlantic, and the California Current in the Pacific, probably influence the regional distributions of *P. triacanthus* and *P. simillimus*, respectively.

P. medius in the Pacific and *P. paru* in the Atlantic seem to parallel one another morphologically and ecologically. Both species are deep-bodied with falcate dorsal and anal fins, but *P. paru* has diverged more sharply to become a very deep-bodied fish with extremely falcate dorsal and anal fins. Although little is known of the habits of *P. medius*, the available evidence suggests that both are essentially shallow-water species that do not migrate seasonally. The geographic ranges are complementary. *P. medius* is distributed from the southern Gulf of California to about 5°S near Paita, Peru, in the eastern tropical-subtropical Pacific and is largely confined within the limits of the 20°C surface isotherms. *P. paru* ranges from just north of Chesapeake Bay to throughout the Gulf of Mexico and the Caribbean region to southern Brazil and also has a tropical-subtropical distribution chiefly within the limits of the 20°C surface isotherms. The opposite pattern of surface currents in the Pacific relative to that in the Atlantic accounts for the disparity in the extent of the tropical-subtropical regions of the two coasts and apparently in the distributions of the two species. Whereas *P. triacanthus* and *P. simillimus* probably acquired temperate adaptations early in the Pleistocene, *P. paru* and *P. medius* seem to have had a continuous warm-water existence. *P. paru* has probably extended its range northward and southward into more temperate waters only since the last glacial period. The species has a continuous distribution around Florida which is indicative of warm-water affinities.

It is possible to postulate two possible mechanisms for the derivation of *P. ovatus*, apparently restricted to the northern Gulf of California. One mechanism is to consider it to have differentiated from *P. simillimus* stock off the outer coast of California and Baja California. C. L. Hubbs (1960) stated that during glacial periods the outer coast fauna was displaced southward to yield Pleistocene relicts in the upper Gulf of California. Walker (1960) counted 22 fish species endemic to the upper Gulf and added that a striking element of the upper Gulf fauna is composed of fishes common to the outer Baja California and southern California coasts, but absent in the extreme southern Gulf. In most cases the degree of differentation is slight. Walker is hesitant to suggest how the northern faunal element reached its present position. He offered the possibility that there may have been a movement through an oceanic connection which existed in the region of the La Paz plain during the late Pleistocene. If movement did occur through such a passage, only a slight general cooling of the waters of the Gulf would have been necessary to allow the entrance of cold-water forms from the outer coast. Because of a temperature front which exists in the cape region, a

much more extensive cooling would seem to be required to allow movement around the cape of Baja California according to Walker.

However, *P. ovatus* is closer to *P. medius* morphologically, and I consider the former species to have been derived from *P. medius* stock even though the mechanism may be less obvious. Derivation from *P. simillimus* would involve an increase in the number of anal rays, in the number of caudal vertebrae, and an increase in body depth, eye size, and depth of caudal peduncle. Derivation from *P. medius* requires a decrease in the number of dorsal rays, in the number of caudal vertebrae, along with an increase in body depth and a decrease in the length of the anterior lobes of the dorsal and anal fins. The latter seems to be a more reasonable and coordinated change of character states and consistent with trends occurring in the genus.

Much of the upper Gulf is quite shallow with wide areas of shelf; the sediment is mostly sand with transition to mud in the delta area of the Colorado River (Walker, 1960). This type of habitat seems suitable for members of this genus, particularly ones closely related to *P. medius*, which seems to be a shallow-water species. Several factors may interact to prevent the southward movement of *P. ovatus* or the northward dispersal of *P. medius* into the upper Gulf: almost the entire Gulf coast of Baja California south of the area mentioned above is rocky, and few stromateid fishes have been collected along this coast; the shelf is narrow in the central Gulf region; temperature and salinity fronts exist in the southern Gulf; two islands with rocky shores are present in the central Gulf with a considerable extent of deep water south of them; increased wind convection and the more extreme ranges of sea surface-temperatures occur in the upper Gulf (Roden, 1958); and, a region of cold water exists around Isla Angel de la Guarda and adjacent islands in the upper central Gulf (Walker, 1960).

P. triacanthus and *P. burti* are the most closely related species in the genus. Their similarity has resulted in different taxonomic interpretations (Caldwell, 1961; Collette, 1963). *P. burti* occupies the now zoogeographically familiar "temperate pocket" of the Gulf of Mexico which in past epochs was continuous with the Atlantic Ocean of the United States because of the submergence of peninsular Florida. Both species are absent as residents from the southern part of Florida, the populations of both forming a disjunct distribution.

C. L. Hubbs (1960) considers the Gulf of Mexico to be geographically and zoogeographically analogous to the Gulf of California in that both contain Pleistocene relicts. Peninsular Florida has been variously submergent and emergent since the Miocene (Cooke, 1945). During the glacial periods of the Pleistocene when the sea level receded, Florida was a peninsula, and conversely, during the high stand of the sea of interglacial periods Florida was in large parts submerged (MacNeil, 1950). Thus, there have been opportunities for junction and disjunction of closely related populations. According to Hedgpeth (1953), the occurrence of nontropical species on both sides of Florida, but not in the southern part of the peninsula, apparently was as characteristic of Pleistocene periods when Florida was a peninsula as it is today. Hedgpeth characterized the Gulf of Mexico as a transitional zone between tropical and temperate regions with environmental conditions favoring invasions from one region or the other at some time during the year. Isothermal configurations presented by Hedgpeth, and studies on the coastal faunas of Florida, show that the southern part of Florida is more tropical than the upper regions. According to Briggs (1958), the shorefish fauna of Florida, particularly the southern element,

has much in common with the fauna of the West Indies, South America, and Bermuda.

The degree of differentiation varies among species which have disjunct populations in the Atlantic and in the Gulf of Mexico. Some have diverged to the species level, others only slightly, and in most cases the decision as to rank is largely arbitrary. The situation has been described for certain species or has been discussed by several authors including Ginsburg (1952), Briggs (1958), R. J. Miller (1959), Caldwell (1961), Collette (1963), and Gutherz (1966) for fishes, and by Hedgpeth (1953) for crabs and molluscs.

The *burti-triacanthus* situation is complex and requires special mention. Caldwell (1961) considered the Atlantic and Gulf populations to be a single polymorphic species, *P. triacanthus*. He recognized three distinct populations of the species: 1) a deep-bodied form in the Gulf of Mexico (equivalent to *P. burti*); 2) a shallow-bodied form in coastal waters of the Atlantic north of Cape Hatteras and in waters usually deeper than 22 m to the south of Cape Hatteras; and 3) a somewhat intermediate form in shallow water of usually less than 22 m in depth south of Cape Hatteras. The Gulf population and the widely-distributed Atlantic population (2 above) are very closely related, but I have found the two forms to be distinct and, in combination with evidence given below, have reinstated *P. burti* as a valid species in the Gulf of Mexico. The morphological differences are in: caudal vertebrae number (17 in *P. burti*, 18–19 in *P. triacanthus*); body depth (Fig. 2); eye diameter (Fig. 3); and, the apparent lack of spots on the body in *P. burti* (Fig. 19) which are frequently present in *P. triacanthus* (Figs. 21 and 22). *P. burti* does not reach the size of *P. triacanthus*, occupies a less extensive depth range than *P. triacanthus* (Table 22), and appears to be less migratory between inshore and offshore waters than *P. triacanthus*.

A main problem is to explain the existence of the shallow-water population in the Atlantic (3 above), which presumably results in two distinct populations of the same species in the Atlantic south of Cape Hatteras. Caldwell (1961) gave two reasons for recognizing two such populations: 1) Mature individuals have been taken from both populations, and there is thus apparently no significant spawning migration; and 2) collections during each season of the year and in almost every month have produced specimens larger than 100 mm SL from most depths. In addition, I have found that most of the deep-water specimens in the Atlantic have been taken largely over a mud or silt bottom in waters up to 420 m depth, while the shallow-water form has been mainly collected over a sand bottom and nearer the coast (Table 22). The shallow-water form is deeper-bodied, usually has 17 or 18 (sometimes 19) caudal vertebrae, apparently has no spots on the body, and agrees closely with the description of *P. burti* (Fig. 19). The deep-water form (Fig. 22) is even more shallow-bodied than more northern members of *P. triacanthus* (Fig. 21), usually has 19 (sometimes 18) caudal vertebrae, and frequently has numerous spots on the body. There is likely some interbreeding between the two populations as evidenced by the overlap in vertebral number; however, the interbreeding is apparently not of the level that would result in the merging of the populations. No external sexual dimorphism or unusual sex ratios have been found in either population.

While it may be possible to explain the development and maintenance of two distinct populations in the same region by considering some type of hybridization, by presuming a strict segregation or divergence as to bottom type, or perhaps by assuming differential growth rates, I tend to favor as an explanatory device the speciation phenomenon of character displacement with the shallow-water population in the Atlantic being a disjunct

element of the Gulf of Mexico species, *P. burti.*

Character displacement may be defined (Brown and Wilson, 1956) as the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened outside this zone. The characters involved may be morphological, ecological, behavioral, or physiological, the situation probably resulting most commonly from the first post-isolation contact of two newly evolved cognate species. Upon meeting, the two populations interact through genetic reinforcement of species barriers, or ecological displacement, or both, in such a way as to diverge further from one another where they occur together. Plasticity of the particular species may result in short-term ecological differences, say in food habits, in situations where species may infrequently come into contact. Whereas, character displacement should be considered as developing over a relatively longer period of time and involving genetic segregation as to morphology, ecology, and other characteristics.

Invoking character displacement requires that the probable history and vagility of the two species be considered. From a knowledge of the history of the genus discussed previously, it seems probable that the Atlantic and Gulf populations have existed since the beginning of the Pleistocene. *P. burti* and *P. triacanthus* or their precursor populations were probably continuously distributed and panmictic during an early interglacial period. A succeeding glacial period would have divided the populations and allowed differentiation and presumably isolating mechanisms to develop. Either during a following interglacial period when contact would have been facilitated, or because of an increased ability to migrate around Florida at some time in the recent past, members of *P. burti* have become distributed in shallow water in sufficient numbers to establish a breeding population in the Atlantic; and, in a first post-isolation contact have morphologically and ecologically displaced the southern members of *P. triacanthus* to the extent that the latter are further offshore, in deeper water, and largely over a mud-silt substrate. Kohn and Orians (1962) have stated that all cases of character displacement should involve displacement of ecological characters since the two species tend to exploit different niches where they occur together.

That these fishes have migrated or can migrate around peninsular Florida or at least are present on both sides of Florida is indicated by at least two pieces of evidence: 1) one record of a fish agreeing in all characters with *P. triacanthus* (especially the southern deep-water form) is known from the southeastern Gulf of Mexico, northeast of the Dry Tortugas (UW 13407); and 2) as has been described, individuals which agree quite closely to the description of *P. burti* have been taken in the Atlantic off Florida (USNM 156149, for example).

It is indeed difficult to advocate character displacement as occurring in the marine environment, especially since so many factors of the interaction cannot be observed or monitored. Although the above explanation is as yet only an hypothesis, the phenomenon of character displacement seems with present evidence to be a reasonable mechanism for explaining the existence of two distinct populations in a given region.

Faunal regions. Much has been written on the extent and delineation of faunal provinces of coastal marine organisms. Often the regions are expanded or contracted to suit the discussion of a particular group of organisms and to allow the greatest number of generalizations. Certain of the faunal boundaries, including ichthyological ones, remain speculative. In the discussion below, no attempt is made to alter the size of the provinces since the

imprecise distributional knowledge of the species does not allow it.

Atlantic Coast. P. paru is distributed throughout the tropical-subtropical region of the western Atlantic and occupies a number of faunal subregions. In ranging from just north of Chesapeake Bay southward throughout the Gulf of Mexico and the Caribbean to southern Brazil, this species is largely confined within the limits of the 20°C surface isotherms (Sverdrup, Johnson, and Fleming, 1942), a boundary often cited for warm-water species. Warm currents flowing away from the equatorial regions result in a relatively wide expanse of tropical and subtropical conditions in the western Atlantic.

The southern limit of *P. paru* seems to concur with the faunal boundary and transition zone which begins at about 23°S in the region of Cabo Frio, Brazil. The partial boundary and transitional area are apparently created by the mixing of the waters of the cold, northward-flowing Falkland Current with those of the warm, southward-flowing Brazil Current, and have been discussed by several South American workers (Balech, 1954; Lopez, 1963; Stuardo, 1964; Vannucci, 1964). *P. paru* ranges southward as far as Buenos Aires, but is less common south of Rio de Janeiro in an area which is largely transitional between the tropical and south temperate regions (Balech, 1954).

P. paru, in the northern part of its range, occupies a somewhat transitional region between subtropical and warm temperate zones.

P. burti and *P. triacanthus* are fishes of more temperate waters than *P. paru*. *P. triacanthus* ranges from the Gulf of Maine to just south of Cape Kennedy, Florida, and thus occupies the so-called Transatlantic Province (Hedgpeth, 1953) which some authors divide into the Virginian, Cape Cod to Cape Hatteras, and the Carolinian, Cape Hatteras to southern Florida. The latter subregion is often considered to be a transitional or mixed zone. Cape Cod is often listed as the southern boundary of the Boreal Province but as Ekman (1953) has indicated, the fluctuating seasonal conditions of temperature in this area make it difficult to define a sharp boundary at Cape Cod. *P. triacanthus* is found seasonally north or south of Cape Cod. This illustrates that water conditions must be of primary importance in zoogeography rather than mere coastal configurations.

P. burti, found throughout the Gulf of Mexico, is a disjunct warm temperate element closely related to *P. triacanthus*. *P. burti* occupies the so-called "temperate pocket" of the Gulf of Mexico.

Pacific Coast. Until recently, two species of *Peprilus*, *P. snyderi* and *P. medius*, were known only from the Gulf of Panama. I have found that both species occupy almost the whole of the tropical-subtropical region of the eastern Pacific. This region extends from the cape region of Baja California to about 6°S off northern Peru near Point Aguja (Ekman, 1953). Ekman includes in this warm-water region the Gulf of California and the Galapagos Islands and regards the area from 3° to 6°S as possibly a transitional zone containing a subtropical fauna. Rosenblatt (1967) considers the southern limit of the tropical region to be at Cabo Blanco, Peru, about 4°S.

P. snyderi occurs as far north as the upper Gulf of California, and Punta San Juanico (about 26°N) on the lower outer coast of Baja California, conforming to C. L. Hubbs' (1960) statement that tropical elements persist much farther north in the Gulf than on the outer coast. This species is not known southward beyond the Gulf of Panama, but it is a rarely-collected species and probably will be found as far south as the Gulf of Guayaquil, Ecuador (about 3°S).

P. medius ranges from the vicinity of Paita, Peru (about 5°S), northward to Bahía Topolobampo (about 25°N) in the southern Gulf of California, thus occupying almost all of the warm-water region.

One uncertain record exists for the Galapagos Islands.

P. simillimus occupies essentially the warm temperate region of the eastern Pacific, but ranges into so-called transitional areas northward and southward. This species occurs from Bahía Magdalena (about 25°N) on the outer coast of Baja California to the southern coast of British Columbia (about 48°N). This species occurs mainly in the Californian Province which extends to about 48°N (Schenck and Keen, 1936). *P. simillimus* is most abundant in an area corresponding closely to the warm temperate San Diegan division of C. L. Hubbs (1960). It is less abundant in the cool temperate division (Montereyan of Hubbs), and even less abundant in the somewhat transitional region between 42°N and 48°N of Schenck and Keen (1936).

In general, the species of *Peprilus* occupy broadly the major faunal regions of the continental shelf. Especially in the warm-water region of the eastern Pacific, the species cross the faunal subregions which have been established mainly from the study of generally small, more restricted fishes of rocky shores such as clinids, gobiesocids, tripterygiids, and chaenopsids (C. Hubbs, 1952; Briggs, 1955; Springer, 1958; Rosenblatt, 1959; and Stephens, 1963).

Degree of divergence in allopatric and sympatric sets of species. Sympatry over an extensive area occurs only in three situations among the seven species of *Peprilus*. The group is somewhat reminiscent of the superspecies concept, superspecies being defined (Mayr, 1963) as a monophyletic group of entirely or essentially allopatric species that are morphologically too distinct to be included in a single species and, thus, that reproductive isolation between them can be assumed.

The genus has a rather narrow ecological diversity. Therefore, it is important to know which species are sympatric and how niche separation is effected in sympatric situations.

Table 26. Values of Coefficient of Difference (C.D.) for Three Pairs of Species of *Peprilus*.

Character (Morphometrics in thousandths of SL)	*burti* / *triacanthus* allopatric	*triacanthus* / *simillimus* allopatric	*triacanthus* / *paru* sympatric
Head length	0.27	0.08	0.31
Snout length	0.12	0.08	0.58
Eye diameter	0.46	0.46	0.56
Upper jaw length	0.22	0.56	0.05
Interorbital width	0.28	0.22	1.01
Pectoral fin length	0.25	0.40	1.06
Predorsal distance I	0.21	0.23	0.81
Predorsal distance II	0.18	0.26	0.63
Preanal distance	0.31	0.10	0.53
Body depth	1.11	0.04	2.34
Caudal peduncle depth	0.34	0.43	1.45
Dorsal rays	0.22	0.15	0.43
Anal rays	0.22	0.28	0.03
Pectoral rays	0.44	0.20	0.62
Gill rakers	0.26	0.05	1.35
Vertebrae	2.39	1.72	2.50
Sum of C.D.	7.28	5.26	14.26
Sum of C.D.*	4.89	3.54	11.76

* Excluding vertebrae.

Coefficients of difference (C.D.) for morphometric and meristic characters were calculated for three pairs of species. The individual and summed C.D. values for each of the either allopatric or sympatric pairs are given in Table 26. The value is obtained by dividing the difference in the means of a character of two populations by the sum of their standard deviations (Mayr, Linsley, and Usinger, 1953: Chapter 7). A value of C.D. which these authors consider to be the conventional level for designating subspecies is 1.28 or above. The method is used here not for subspecific distinctions, but to show that generally in the genus *Peprilus* the diverse sets of species are sympatric and the similar ones allopatric.

P. snyderi and *P. medius* are sympatric

throughout much of the warm-water region of the eastern Pacific. They have been taken in the same hauls and are members of different species groups. *P. snyderi* is the more rarely collected of the two species, and although the data are meager, it seems to be a more vagile fish and one more frequently in deep water than *P. medius*. Collections of the latter species are mostly from shallow coastal areas and bays.

P. snyderi and *P. simillimus*, two quite similar species (Table 21), are sympatric in a small region on the outer coast of Baja California; however, there is only one record of *P. snyderi* from this region. I believe that the two species very rarely come in contact, especially during the breeding season. *P. snyderi* probably breeds only farther south along the Mexican coast. *P. simillimus* replaces the tropical *P. snyderi* northward in temperate waters.

One record exists for *P. snyderi* in the upper Gulf of California where it would come in contact with the considerably dissimilar *P. ovatus*. *P. snyderi* is apparently quite rare in this region, also.

P. snyderi differs noticeably from *P. medius* and *P. ovatus*, but less so from *P. simillimus* (Figs. 2–6; Table 21). The differences seem to reflect the acquisitions associated with the trend toward a deep, short body in *P. ovatus* and *P. medius*, and include a larger eye, deeper body, slightly longer pectoral fin, and deeper caudal peduncle. These differences may be correlated with an existence in a shallow, essentially inshore habitat. The longer pectoral fin, shorter body, and deeper caudal peduncle seem suited for short-distance, nonmigratory swimming, and the larger eye an adaptation for living continuously in highly productive, but less transparent inshore waters.

In the Atlantic *P. paru* is sympatric with *P. burti* and with *P. triacanthus*, except in the northern portion of the range of the latter. *P. paru* best exemplifies the trend within the genus toward a short, deep body (Table 21; Figs. 2–6). It is a shallow-water, inshore species while *P. triacanthus* and *P. burti* seasonally migrate between inshore and offshore waters and are more regularly in deeper water.

The premaxillary teeth of *P. triacanthus* and *P. burti* each have three small cusps (Fig. 33b) while those of *P. paru* and the rest of the species are generally simple and pointed (Fig. 33a). The teeth of the lower jaw of all the species of *Peprilus* are multicusped but the cusp pattern in *P. burti* and *P. triacanthus* is slightly different. The significance of these differences in the teeth is as yet unknown; however, they may indicate a slight difference or segregation in food habits between say, *P. paru* and *P. triacanthus*. Mouth size (Fig. 4) and, apparently, food habits are similar among the species.

The above comparisons show that sympatry involves the more diverse sets of species, whereas the sets or pairs of species which are very similar tend to parallel one another in different oceans or to replace one another in adjacent faunal regions with perhaps a small area of sympatry or none at all. Niche separation is to a considerable degree effected spatially, i.e., one species in shallow water and a second ranging over a more extensive area of the shelf and generally in deeper water. There may be some shifts in food habits among sympatric forms or some type of resource subdivision, although no differences in diet among species have been discovered. This apparent similarity in food habits further suggests that spatial arrangement and ecological displacement are important in niche separation.

The nature of speciation in the genus Peprilus. Most of the differentiation and speciation in the genus seems to have taken place since the emergence of the Central American land bridge in the Pliocene. Before the emergence, the tropical faunas of the eastern Pacific-western Atlantic were apparently continuous and

homogeneous. Rates of evolution in the group are difficult to estimate since there is substantial difference of opinion as to the time in the Pliocene when the land bridge was completely formed. Briggs (1967), in following Simpson's (1950) statement that the Isthmus of Panama made its last emergence in the latest Pliocene or earliest Pleistocene, estimates an age of one and one-half million years for the Central American barrier. Schuchert (1935) and Durham and Allison (1960) consider the time of emergence as the early Pliocene (or perhaps the late Miocene according to a reference of the latter authors). With the length of Pliocene as approximately ten million years (Kummel, 1961), a discrepancy of perhaps six to eight million years exists for the time of isolation of the Atlantic and Pacific faunas, depending upon whether one considers the early Pliocene or the late Pliocene as the date of closing of the seaway. Ira Rubinoff (personal communication) favors a period of three to four million years as the length of time since the effective separation of the Atlantic and Pacific shore faunas.

In general, the isolation of the two faunas has resulted in divergence to the species level, which may indicate the later closure of the seaway since the average age of a species might cautiously be considered to range from 100,000 to a few million years (Rensch, 1959). Rosenblatt (1967) finds that the shorefish faunas of the two sides of the Americas exhibit profound similarities on the familial, subfamilial, and generic levels, but that few species are common to both coasts. According to Briggs (1967), only about 12 of the approximately 1000 fish species along the tropical American coasts are still identical, making the Central American barrier 99 per cent effective. Members of the genus *Peprilus* conform to this pattern in that the genus is found on both coasts, but none of the species occur on both sides.

The members of the genus have considerably higher vagility and a greater ability for genetic interchange over a broad geographic region than do a number of other coastal fishes, particularly those of rocky shores. The fishes of this genus possess considerable ability not only for active dispersal but for passive disperal as well via the planktonic stages of eggs and larvae. They are of medium size (smaller than 300 mm in length) and have a life span of several years (at least three or four years), characteristics which should contribute to the maintenance of genetic interchange and a certain homogeneity within a particular species. In contrast, the controlling factors in the distribution of fishes of rocky littoral areas are more restrictive and localizing in nature. Rosenblatt (1963) states that fishes of rocky shores and coral areas are usually small, short-lived (perhaps one or two years), often territorial, and either have a short pelagic larval period or are even viviparous as is characteristic of a number of families of rocky littoral zones. He reasons that these factors curtail gene flow, frequently change the composition of the gene pool, and lead to differences in gene frequency either randomly or in response to local conditions. Such a population structure is favorable for the fragmentation of a species and the evolution of new species. The genus *Peprilus* and similar genera with wide-ranging coastal species are usually much less speciose than genera of rocky shores, and usually traverse the zoogeographic subregions occupied by fishes of rocky littoral areas.

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SUMMARY

A revision is presented of the genus *Peprilus*, one of the three genera of the family Stromateidae. The nominal genera *Poronotus* and *Palometa* are placed in the synonymy of *Peprilus*. Seven species are recognized in the genus. *P. ovatus* is described as a new species and is apparently restricted to the northern Gulf of California. *P. medius* and *P. palometa* are synonyms, and the former is the valid name. *P. alepidotus* is treated as a synonym of *P. paru*. Accounts of each species consist of a synonymy, diagnosis, description, distribution, the geographic variation, and the ontogenetic change.

The genus *Peprilus* occurs in tropical and temperate waters along the coasts of North, Central, and northern South America. Four species, *P. medius, P. ovatus, P. simillimus*, and *P. snyderi*, are distributed along the Pacific Coast, and three, *P. triacanthus, P. burti*, and *P. paru*, along the Atlantic Coast.

Several aspects of functional morphology are considered. The vertebral column, skull, and pectoral fins appear to ossify earlier than the caudal skeleton and median fins, a sequence interpreted as being correlated with an early planktonic life followed by an independent nektonic existence. Vertebral number is relatively constant within a species and is considered to be of possible selective value in maintaining a certain body form. The absence of pelvic fins, the long pectoral fins which are used extensively for propulsion in adult fishes, and the compressed body may all be correlated with the continuous swimming habit of these fishes, especially those larger than 100 mm SL. An hypothesis is presented that the swimbladder is of hydrostatic advantage to juvenile fishes which hover under jellyfish medusae and that it becomes nonfunctional in larger fishes which swim continuously. The scales are highly deciduous, and the skin is underlain by an extensive canal system, the function of which is unknown. The alimentary canal is composed of a small mouth with nipping teeth, a toothed, muscular pharyngeal sac, a U-shaped stomach, numerous pyloric caeca, and a long intestine. The food is shredded in the pharyngeal sac, and the great absorptive area of the caeca and intestine probably allows for maximum utilization of jellyfish and other food items.

Considerations of life history and ecology are generally of four species – *P. triacanthus, P. burti, P. paru*, and *P. simillimus*. Spawning occurs in the pelagic surface layers at varying distances from shore. The eggs and larvae are planktonic, the latter becoming capable of independent locomotion at a size of about 10 to 15 mm SL. The species occur in a wide range of salinity and variously inhabit all depths over the continental shelf and generally over a sand or mud bottom. The genus is essentially tropical and warm temperate, with only two species, *P. triacanthus* and *P. simillimus*, reaching cooler waters. Seasonal movements appear to be most pronounced in *P. triacanthus*, the species occurring most abundantly in temperate regions. Fishes smaller than 100 mm SL associate with jellyfish medusae of several

genera. This association is apparently important during the early critical growth phases of the fishes. *Peprilus* is a low-level carnivore; jellyfish medusae seem to be an important element in the diet, especially of juveniles. Other food items include a variety of small crustaceans, polychaete worms, and small fishes. Members of the genus are evidently significant forage fishes for a number of larger fishes, some of which are of great commercial importance. The economically important species of *Peprilus* are generally taken commercially in a region much smaller than the total range of the species, and this seems to reflect the pattern of migration and center of abundance of the particular species.

Disruption of the Tethys Sea in the Miocene apparently facilitated the segregation of the early members of the family Stromateidae and led to the evolution of the three extant and essentially allopatric genera. The formation of the Central American land bridge in the Pliocene, the emergence and submergence of land areas associated with the Pleistocene glacial and interglacial periods, and the prevailing current systems all appear to have been important in producing the current level of differentiation and speciation in the genus.

The elongate *P. snyderi* is considered to be the most primitive type and the deep-bodied *P. paru* the most highly derived form in the genus. The Camin-Sokal method for deducing relationships of contemporaneous species is used to reconstruct a dendrogram of species relationships. Two somewhat subtle species groups are recognized in the genus, and each group is represented on both sides of the Central American isthmus. Character displacement is invoked as a possible mechanism to explain the existence of two apparently distinct populations of *P. triacanthus* in the Atlantic off the southeastern coast of the United States.

The distribution of the species of *Peprilus* appears to correspond generally to the major faunal provinces of the Atlantic Coast and the Pacific Coast of the Americas. The species generally traverse the zoogeographic subdivisions established from the study of small fishes inhabiting rocky shores. Sympatry involves the more diverse species, and the similar or closely related species tend to parallel one another in different oceans or displace one another latitudinally along a continuous coastline. Niche separation seems to be produced largely by spatial arrangement and ecological displacement.

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THE SYSTEMATICS AND ZOOGEOGRAPHY OF THE UNIONIDAE (MOLLUSCA: BIVALVIA) OF THE SOUTHERN ATLANTIC SLOPE REGION

RICHARD I. JOHNSON

CONTENTS

Introduction 264

Acknowledgments 266

Part I. The zoogeography of the Unionacea of the Apalachicolan and Atlantic Slope regions 267

Chapter 1. The distribution of the Unionacea in the Apalachicolan region as evidence of a former confluence of the headwaters of the Alabama-Coosa, Apalachicola, and Savannah river systems 267

The Apalachicolan region defined 267

Analysis of the distribution of the species 268

Chapter 2. The distribution of the Unionidae in the Southern Atlantic Slope region as evidence of a former stream confluence of the headwaters of the Apalachicola and Savannah river systems 273

The Atlantic Slope region defined and subdivided 273

Analysis of the distribution of the species 275

Chapter 3. The Unionacea of the Northern Atlantic Slope region, with a discussion of the probable origin of some of the Atlantic slope species 278

Analysis of the distribution of the species 278

Chapter 4. The generic affinities of the Unionacea of the Apalachicolan region, Peninsular Florida, and Southern and Northern Atlantic Slope regions 281

Chapter 5. The relationship of the geomorphology and topography of the Apalachicolan and Atlantic Slope regions to their unionid faunas 283

Evidence of stream capture 284

The Piedmont Plateau 285

The Coastal Plain 286

Chapter 6. Summary and Conclusions 291

Part II. A revision of the Unionidae from the St. Marys River, Florida, to the Potomac River, Maryland 293

Introduction 293

History of the taxonomists and the collectors of the Atlantic Slope Unionacea 293

The taxonomists 293

The collectors 294

The primary systematic studies of Apalachicolan and Atlantic Slope Unionacea 294

Classification of the Unionacea 295

Systematic Section 296

Key to the Unionidae found between the St. Marys River, Florida, and the Potomac River, Maryland 297

PLEUROBEMA 299

Lexingtonia 300

Pleurobema (Lexingtonia) collina (Conrad) 300

Pleurobema (Lexingtonia) masoni (Conrad) 301

ELLIPTIO 303

Canthyria 303

Elliptio (Canthyria) spinosa (Lea) 303

Elliptio s. s. 304

Elliptio (Elliptio) crassidens crassidens (Lamarck) 305

Elliptio (Elliptio) crassidens downiei (Lea) ... 307
Elliptio (Elliptio) congaraea (Lea) ... 308
Elliptio (Elliptio) dariensis (Lea) ... 310
Elliptio (Elliptio) fraterna (Lea) ... 312
Elliptio (Elliptio) waccamawensis (Lea) 313
Elliptio (Elliptio) complanata (Lightfoot) ... 314
Elliptio (Elliptio) hopetonensis (Lea) 324
Elliptio (Elliptio) icterina (Conrad) ... 325
Elliptio (Elliptio) arctata (Conrad) ... 331
Elliptio (Elliptio) lanceolata (Lea) ... 333
Elliptio (Elliptio) shepardiana (Lea) 338
UNIOMERUS ... 339
Uniomerus tetralasmus (Say) ... 339
LASMIGONA ... 343
Platynaias ... 343
Lasmigona (Platynaias) subviridis (Conrad) ... 343
ALASMIDONTA ... 346
Prolasmidonta ... 346
Alasmidonta (Prolasmidonta) heterodon (Lea) ... 347
Alasmidonta s. s. ... 348
Alasmidonta (Alasmidonta) undulata (Say) ... 349
Alasmidonta (Alasmidonta) triangulata (Lea) ... 351
Alasmidonta (Alasmidonta) arcula (Lea) 352
Decurambis ... 353
Alasmidonta (Decurambis) varicosa (Lamarck) ... 354
ANODONTA ... 356
Pyganodon ... 356
Anodonta (Pyganodon) cataracta cataracta Say ... 356
Anodonta (Pyganodon) gibbosa Say ... 359
Anodonta (Pyganodon) implicata Say 360
Utterbackia ... 362
Anodonta (Utterbackia) imbecilis Say 362
Anodonta (Utterbackia) couperiana Lea 365
STROPHITUS ... 366
Strophitus undulatus (Say) ... 367
CARUNCULINA ... 369
Carunculina pulla (Conrad) ... 370
VILLOSA ... 371
Villosa villosa (Wright) ... 372
Villosa vibex (Conrad) ... 373
Villosa delumbis (Conrad) ... 375
Villosa constricta (Conrad) ... 378
LIGUMIA ... 380
Ligumia nasuta (Say) ... 380
LAMPSILIS ... 382
Lampsilis s. s. ... 382
Lampsilis (Lampsilis) cariosa (Say) ... 382
Lampsilis (Lampsilis) dolabraeformis (Lea) ... 384
Lampsilis (Lampsilis) ovata (Say) ... 386
Lampsilis (Lampsilis) ochracea (Say) 388
Lampsilis (Lampsilis) radiata radiata (Gmelin) ... 390
Lampsilis (Lampsilis) splendida (Lea) 393
Bibliography ... 395
Index to relevant taxa ... 399

ABSTRACT

The Atlantic Slope region consists of those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, including rivers in Newfoundland and Labrador. Forty species comprise the unionid fauna. Most of the species that are clearly of Interior Basin origin are a northern group that migrated around the northern end of the Appalachian Mountains before the Pleistocene; there is a southern group that entered the Atlantic Slope region through a confluence of the Apalachicola and Savannah river systems, also in pre-Pleistocene time; there is also an additional fauna originally of Interior Basin origin, but whose ancestry is more remote.

INTRODUCTION

The Unionacea and Mutelacea (Parodiz and Bonetto, 1963), or freshwater mussels, are found throughout the world, but it is in the Mississippi River system that the Unionidae have especially radiated and achieved their greatest diversity. This, the *Interior Basin,* embraces 1,200,000 square miles. The rivers are very old, and flow over vast limestone beds. Here is found a variety of shell forms which is rivaled only in a few species found in the rivers of

China. Within the Interior Basin, H. and A. van der Schalie (1950: 450) recognized the *Ozark* and *Cumberland* regions, each of which has an indigenous unionid fauna of its own, as well as the Interior Basin one.

Continental North America is made up of the following additional regions. They are given essentially as defined by H. and A. van der Schalie (1950). The *Pacific* region is the area west of the Rocky Mountains. It has a very limited unionid fauna, which is clearly of Asiatic origin. Found there are several species of *Anodonta*, *Margaritifera margaritifera* (Linnaeus), and *"Gonidea" angulata* (Lea), which may belong to the Asiatic genus *Solenaia* Conrad.

The *West Gulf Coastal* region consists of the streams flowing into the Gulf of Mexico from the eastern slope of Mexico north to, but not including, the Alabama-Coosa River system. Found there are several endemic genera of Unionidae. It has been tentatively suggested by both Simpson (1892: 406) and H. and A. van der Schalie (1950: 452) that this might be regarded as a subregion of the Interior Basin.

The *Apalachicolan* (or *West Floridian*) region was mentioned by H. and A. van der Schalie (1950: 450) and is now defined as consisting of those river systems flowing into the Gulf of Mexico from the Escambia to the Suwannee, and also including the St. Marys and the Satilla, which flow directly into the Atlantic Ocean.

Peninsular Florida has representatives of only six genera. These consist of species derived mostly from the Apalachicolan and Atlantic Slope regions. This area will be discussed as a separate region in a subsequent report.

The *Atlantic Slope* region includes the river systems flowing into the Atlantic Ocean from the Altamaha, Georgia, to the lower St. Lawrence, Canada, as well as those of Newfoundland and Labrador. The Unionidae of this region are of Interior Basin origin, but on the Atlantic slope the species are smaller and are neutral in color. Yet, the only two species of Unionidae with true spines, *Elliptio spinosa* (Lea) and *Pleurobema collina* (Conrad), occur here.

Because the Atlantic Slope region has distinct northern and southern assemblages of species, it has been divided here into the *Southern Atlantic Slope* region, which extends from the Altamaha River system, Georgia, to the James River system, Virginia, and the *Northern Atlantic Slope* region, which extends from the York River system, Virginia, to the lower St. Lawrence River system, Canada. Between the York River and the glacial drift border (roughly along the Pennsylvania-New York boundary) are found all of the Unionacea that repopulated the Northern Atlantic Slope region north of the limit of glacial drift.

The Unionacea, or freshwater mussels, offer two advantages for zoogeographic study: 1) As shown in the systematic portion of this paper, there are a reasonable number of species, most of which are clearly distinguishable, and whose generic affinities have been revealed rather clearly by Ortmann (1911; 1912a). 2) They have a limited mode of distribution, being unable to pass over land from one drainage system to another. Their ability to move between drainage systems is dependant on the mobility of fishes to which the glochidia attach themselves. Of the primary freshwater fishes, Myers (1938: 343) stated,

> "They are inescapably confined to their own particular drainage systems and can migrate from one isolated stream basin to the next only through the slow physiographical change of the land itself (stream capture, etc. [base-leveling])."

For this reason the distribution of the Unionacea gives evidence of former stream confluences and of flooding in baseleveled coastal regions.

Van der Schalie (1945) convincingly illustrated the use of Unionidae as a means of tracing major stream confluences. He also reviewed the old controversy over mechanical distribution, which implies that

unionid distribution is haphazard and fortuitous, caused by aquatic birds to whose feet gravid females may occasionally become attached. This theory postulates that the shell will be carried to a different river system, and that there the glochidia will be released and will find a *suitable* host fish. No one has actually established that Unionidae have been successfully spread by birds in this manner, but even granting this possibility, there is no evidence that it is, or was, an important method of distribution, since zoogeographic data fail to substantiate unionid distribution by any agent other than fish.

In their discussion of the freshwater mollusks of the Apalachicolan region, Clench and Turner (1956: 103) support the idea that that fauna was distributed by mechanical means, though they are vague as to what those means might have been. Exception is taken here to their theory of distribution, but *only* as far as the Unionacea are concerned.

The Apalachicolan Unionacea were restudied, and it is demonstrated here that their general distribution is not fortuitous. References are made to some of the Unionidae of the Alabama-Coosa River system to illustrate the origin of some of the Apalachicolan species and to illuminate the sequence of stream captures which affected the distribution of both Apalachicolan and Southern Atlantic Slope Unionidae.

In his classic study of the influence of the Alleghenian Divide on the distribution of mollusks and crayfish, Ortmann (1913a) assumed that the Unionidae were distributed by natural means. Both by choice and because of the confusion in which he found the systematics of the southern species, his work was limited to the Atlantic side of the divide, primarily to the species of Unionacea found on the Northern Atlantic slope.

In the present study, the distribution of the Apalachicolan and Atlantic Slope Unionacea is analyzed, and, with the exception of *Margaritifera margaritifera* (Linnaeus), *Alasmidonta marginata* (Say), and *Anodonta cataracta fragilis* (Lamarck), which are beyond the scope of this paper, all of the Atlantic Slope Unionacea are included and their nomenclature is revised.

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In 1961, Dr. William J. Clench, my longtime mentor, received a grant from the National Science Foundation (G18922) to make a collection of the freshwater mollusks of the Atlantic Slope of Georgia. Upon completion of the expedition, he generously gave me the Unionidae for study. As the study progressed, it gradually became apparent that the unionids of the entire Southern Atlantic slope had to be included if the work was to be of any significance.

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material collected by Mr. Fuller in the Museum of Comparative Zoology.

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PART I. THE ZOOGEOGRAPHY OF THE UNIONACEA OF THE APALACHICOLAN AND ATLANTIC SLOPE REGIONS

CHAPTER 1

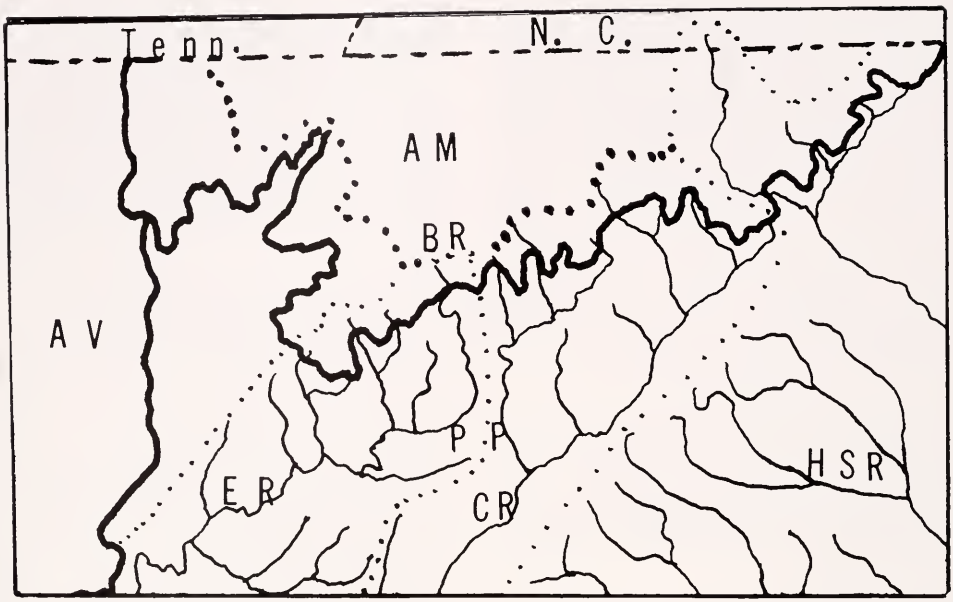
The distribution of the Unionacea in the Apalachicolan region as evidence of a former confluence of the headwaters of the Alabama-Coosa, Apalachicola, and Savannah river systems.

Figure 1 illustrates the propinquity of the headwaters of the Alabama-Coosa, Apalachicola, and Savannah river systems. Van der Schalie (1945) made it clear that there was once a connection between the Tennessee and Alabama river systems; this connection is of interest here since certain unionid species of the Alabama-Coosa River system are discussed in this paper. Matteson (1948a: 131) following, in part, Hayes and Campbell (1894), suggested that in the late Tertiary, the Chattahoochee River of the Apalachicola River system captured a tributary of the Etowah River, of the Alabama-Coosa River system, and that the Savannah River then captured one of the tributaries of the Chattahoochee River. This present study supports these geomorphological assertions, but in a different order. The distribution of Apalachicolan species in the Savannah River system seems to indicate that this system may first have been connected to, and later separated from, the Chattahoochee River before the latter was connected to the Alabama-Coosa River. These conditions would explain why certain species found in both the Alabama-Coosa and Apalachicola river systems are absent in the Savannah River system.

To understand the origins of the Unionidae of the Southern Atlantic Slope, it was necessary to study the distribution of the superfamily Unionacea in the Alabama-Coosa and Apalachicola river systems. Further, the whole Apalachicolan region had to be considered, to determine if it could be established that unionid distribution there is not fortuitous.

The Apalachicolan region defined. This region is regarded here as consisting of the river systems flowing into the Gulf of Mexico, from the Escambia to the Suwannee. Also included are the St. Marys and Satilla, although they flow into the Atlantic Ocean (Plate 1), because, as Table 1 shows, their modest unionid faunas consist entirely of species found in the Apalachicolan region, and further, because *Elliptio crassidens crassidens* and *E. c. downiei* occur in them, respectively, and are dominant.

According to Cooke (1945: 273), in the early Pleistocene, during the Aftonian interglacial stage when the Brandywine terrace (Citronelle Formation in the Southeast) was formed, the sea level was 270 feet above the present level. If this were so, most of the area occupied by the present St. Marys and Satilla river systems, and virtually all of Peninsular Florida, were inundated, with the exception of



Text-figure 1. Northern Georgia, illustrating the propinquity of the headwaters of the Etawah River (ER), of the Alabama-Coosa; of the Chattahoochee River (CR), of the Apalachicola; and of the Savannah (HSR) river systems. The topographic areas are the Appalachian Mountains (AM), Appalachian Valley (AV), and the Piedmont Plateau (PP). The Blue Ridge divide (BR) is indicated by large dots. The minor divides are indicated by smaller dots. (After Keith, 1925, pl. 29.)

several small islands in the vicinity of present Polk County (Cooke, 1945: 273).[1]

It is now generally agreed that this flooding took place in the Upper Miocene (Alt and Brooks, 1965: 408).

MacNeil (1950: 98, 99) casts doubt on Cooke's evidence on the extent of Aftonian flooding, and on the basis of his identification of marine terraces concludes that the Citronelle Formation is of subaerial origin, and that there is no evidence to indicate that the sea ever transgressed it to an altitude of more than 150 feet during the Yarmouth interglacial stage. This flooding is now thought to have occurred during the Pliocene. MacNeil's detailed map (pl. 19) shows that even at 150 feet Peninsular Florida was reduced to a number of small islands where a unionid fauna might have had refugia. In any case, except for a small portion of the Satilla River which is above the area of maximum flooding, the remainder of it, and all of the St. Marys River, is of more recent origin (see p. 289).

It is assumed that these two rivers were mostly repopulated from the west. The appearance of *Elliptio c. crassidens* in the Pliocene of Florida (see note on p. 271) indicates that it has been present in this general area over a long period of time.

Analysis of the distribution of the species.

The Apalachicolan and Atlantic Slope regions consist of a number of independent river systems, some with quite different faunas. Table 1 shows all of the Unionacea known from the individual Apalachicolan river systems, systematically arranged. Some differences in species concepts and

[1] Orange (Ocala) Island, referred to by Clench and Turner (1956: 104), was a land mass that was separated from the continent by the Suwannee Strait during the late Oligocene (Vaughan, 1910: 156), and its existence appears to have had no bearing on the present unionid fauna.

TABLE 1. DISTRIBUTION OF THE UNIONACEA OF THE APALACHICOLAN REGION AND RELEVANT SPECIES OF THE ALABAMA-COOSA RIVER SYSTEM.

Alabama-Coosa River system		Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
	1. *Margaritifera hembeli* (Conrad)	×							
1/	2. *Fusconaia succissa* (Lea)	×	×	×					
	3. *Fusconaia escambia* Clench & Turner	×	×						
	4. *Quincuncina infurcata* (Conrad)				×	×	×		
	5. *Quincucina burkei* Walker			×					
×	6. *Amblema boykiniana* (Lea)	×			×	×			
	7. *Amblema neisleri* (Lea)				×				
×	8. *Amblema perplicata** (Conrad)	×	×						
2/	9. *Pleurobema strodeanum* (Wright)	×	×	×					
	10. *Pleurobema pyriforme* (Lea)				×	×	×		
×	11. *Elliptio crassidens crassidens* (Lamarck)	×			×			×	
	12. *Elliptio crassidens downiei* (Lea)								×
	13. *Elliptio fraterna* (Lea)			×	×				
3/	14. *Elliptio complanata* (Lightfoot)				×				
	15. *Elliptio icterina* (Conrad)	×	×	×	×	×	×	×	
×	16. *Elliptio arctata* (Conrad)	×	×		×				
	17. *Elliptio lanceolata* (Lea)	×			×				×
	18. *Elliptio jayensis* (Lea)					×	×		
	19. *Elliptio nigella* (Lea)*				×				
	20. *Elliptio chipolaensis* (Walker)				×				
	21. *Elliptio sloatiana* (Lea)				×	×			
×	22. *Uniomerus tetralasmus* (Say)	×	×	×	×	×	×		
4/	23. *Alasmidonta triangulata* (Lea)				×				
	24. *Alasmidonta wrightiana* (Walker)*					×			
×	25. *Anodonta grandis* Say			×	×	×			
×	26. *Anodonta cataracta cataracta* Say			×	×				
×	27. *Anodonta imbecilis* Say	×			×	×			
	28. *Anodonta peggyae* Johnson*			×	×	×	×		
	29. *Anodonta couperiana* Lea				×	×		×	
	30. *Anodonta suborbiculata* Say*	×							
×	31. *Anodontoides radiatus* (Conrad)*	×			×				
×	32. *Strophitus subvexus* (Conrad)*				×				
5/	33. *Obovaria rotulata* (Wright)*	×							
×	34. *Carunculina parva* (Barnes)	×	×	×	×	×	×		
×	35. *Villosa vibex* (Conrad)	×	×	×	×	×	×		
×	36. *Villosa lienosa* (Conrad)	×	×	×	×	×	×		
	37. *Villosa choctawensis* Athearn*			×					
	38. *Villosa villosa* (Wright)				×	×	×	×	
×	39. *Lampsilis excavatus* (Lea)	×							
×	40. *Lampsilis claibornensis* (Lea)	×	×	×	×	×	×		
	41. *Lampsilis haddletoni* Athearn*			×					
	42. *Lampsilis binominatus* Simpson*				×				
×	43. *Lampsilis anodontoides* (Lea) (6)	×		×	×	×	×		
	44. *Lampsilis australis* Simpson	×		×					
	45. *Lampsilis jonesi* van der Schalie*			×					

TABLE 1. (*Continued*)

Alabama-Coosa River system		Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
	46. *Lampsilis subangulata* (Lea)				×	×			
×	47. *Medionidus penicillatus* (Lea)				×				
	48. *Medionidus walkeri* (Wright) (7)				×	×	×		
×	49. *Glebula rotundata* (Lamarck)	×			×				
	TOTAL NUMBER OF SPECIES	23	11	18	33	20	13	4	2

* (See Johnson, 1965; 1967b,c; 1968; 1969a). *A. perplicata* (Conrad) has not been previously published on as part of the Apalachicolan fauna. It has been found in the Escambia River, Pine Barren, Escambia Co., Florida, and in Picket Retch Lake [not located, but presumed to be in the Yellow River system], Walton Co., Florida.

1. *Fusconaia*, represented by several species.
2. *Pleurobema rubellum* (Lea).
3. *Elliptio dilatata* (Rafinesque) see p. 279.
4. *Alasmidonta mccordi* Athearn (1964: 134, pl. 9, figs. a–b). Not close to *Alasmidonta s.s.*
5. *Obovaria unicolor* (Lea).
6. Clench and Turner (1956: 158), following Simpson (1914: 91), recognize *floridensis* (Lea) as a subspecies of *Lampsilis anodontoides* (Lea) = *teres* (Rafinesque), but admit that "young specimens of the typical form would be difficult to separate from this subspecies." It is true that specimens of this species tend to be smaller and thinner toward the southern end of its range, but *floridensis* is not a subspecies as this concept is currently understood. It was described as: *Unio floridensis* Lea 1852. Trans. Amer. Philos. Soc. 10: 274, pl. 21, fig. 31 [Cháctáhachi River, West Florida, figured holotype ANSP 42081. Clench and Turner (1956: 202) restricted the type locality to the Choctawhatchee River, 1 mi. W Caryville, Holmes Co., Florida]. Lea, 1852, Obs. Unio, 5: 30.
7. Clench and Turner (1956: 189, pl. 6, fig. 7), under the name *Medionidus penicillatus* (Lea), described and figured *Medionidus walkeri* (Wright), a species endemic to the Apalachicolan region having a well defined posterior ridge and a posterior slope with strong corrugations that run from the posterior ridge to the posterior margin.

Medionidus penicillatus (Lea), though found in the Apalachicolan region, is more common in the Alabama-Coosa River system. It has a very rounded posterior ridge, and a posterior slope that has, when sculpture is present, small, slightly curved folds that run from the posterior ridge to the posterior margin. It was described as: *Unio penicillatus* Lea 1857, Proc. Acad. Nat Sci. Phila., 9: 171 (Chattahoochee River, near Columbus [Muscogee Co.]; [Chattahoochee River], near Atlanta [De Kalb Co.]; Flint River near Albany, [Dougherty Co.]; *all* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 203, pl. 23, fig. 85, figured holotype USNM 84142 from the Flint River. Clench and Turner (1956: 190) restricted the type-locality to the Chattahoochee River, near Columbus). Lea, 1859, Obs. Unio., 7: 21.

nomenclature from that of Clench and Turner (1956) were noted by Johnson (1965; 1967b, 1967c; 1968; 1969a); the remainder are discussed in the notes to Table 1, or in the systematic portion of this paper.

Because of its former connection with the Tennessee River, the unionid fauna of the Alabama-Coosa River system is extensive. Only those genera and species that seem germane to the understanding of the distribution of the Unionacea of the Apalachicolan and Atlantic Slope regions are included here.

Forty-nine species comprise the unionid fauna of the Apalachicolan region (Table 1); nineteen species have affinities with species to the west, twelve are endemic to the region, and eleven more are restricted to individual river systems. Three species, which were probably originally endemic to the Apalachicolan region, have spread into the Atlantic Slope region, and four others have spread in the opposite direction.

Six Apalachicolan unionids are so ubiquitous throughout the region (Table 1, A) that they offer no clues as to their method of distribution. *Amblema perplicata* (Conrad) is found in rivers flowing into the Gulf of Mexico from central Texas to the Yellow River system, Florida, and in the west, north to river systems in Arkansas and Missouri. It is close to *A. plicata* (Say), which is widely distributed throughout the Interior Basin. *Lampsilis excavatus* ranges uniformly from the Pearl River, Mississippi, to the Escambia River system, Florida. *Margaritifera hembeli*, a member of the family Margaritiferidae, appears to be a relict. It is found in one other drainage, the Bayou Teche, Louisiana, in the West Gulf Coastal region. *Anodonta suborbiculata* is widely distributed throughout the Interior Basin.

Table 1, A. Unionacea, derived from the west, found in the Alabama-Coosa River system, and which terminate in the Apalachicolan region, or are widely distributed throughout and beyond it.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida	Southern Atlantic Slope
U. tetralasmus	×	×	×	×	×	×			×	×
C. parva	×	×	×	×	×	×			×	
L. claibornensis	×	×	×	×	×	×				
V. vibex	×	×	×	×	×	×			×	
V. lienosa	×	×	×	×	×	×			×	×
L. anodontoides	×	×	×	×	×	×			×	
A. perplicata	×	×								
L. excavatus	×									
M. hembeli	×									
A. suborbiculata	×									

Nine species of the Alabama-Coosa River system (Table 1, B) appear to have reached the Apalachicola River through a former stream confluence (Text-fig. 1, see p. 285), since they are mostly missing from intervening systems. With the probable exception of *Anodonta grandis*, *A. imbecilis*, and *Glebula rotundata*, it is possible that the remaining six species were once endemic to the Alabama-Coosa River system. Matteson (1948a: 131) suggests that *Elliptio c. crassidens* and *E. dilatata* Rafinesque (figured by Ortmann, 1919: 95, pl. 8, fig. 2) reached the Interior Basin from the Alabama-Coosa River system. If this can be shown, then *Elliptio s. s.* is a genus originally from the coastal regions.

Four species of Unionidae appear to have reached the Apalachicolan region from a former confluence of the Apalachicola and Savannah river systems (Table 1, C). They will be discussed with the Southern Atlantic Slope fauna. Three additional species entered the Savannah

Table 1, B. Unionidae, derived from the west, found in both the Alabama-Coosa and Apalachicola river systems, supporting the assumption of a former confluence between them.

	Alabama-Coosa River system	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida
E. crassidens	×	×			×			×		×[1]
A. boykiniana	×	×			×	×				
A. grandis	×			×	×	×				
A. imbecilis	×	×			×	×				
E. arctata	×	×	×		×					
A. radiatus	×	×			×					
S. subvexus	×				×					
G. rotundata	×	×			×					
M. penicillatus	×				×					

[1] *E. crassidens* has been found as a fossil in the Pliocene deposits of St. Petersburg, Hillsboro Co., Florida. It was renamed *Elliptio pachyodon* Pilsbry (see p. 306).

TABLE 1, C. UNIONIDAE, DERIVED FROM THE EAST OR WEST, FOUND IN THE ALABAMA-COOSA AND APALACHICOLA RIVER SYSTEMS, AND WHICH GIVE EVIDENCE OF A FORMER CONFLUENCE WITH THE SAVANNAH RIVER SYSTEM, INCLUDING THE POSTULATION OF TWO MINOR STREAM CONFLUENCES.

		Alabama-Coosa River system	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida	Savannah River system
From West	*E. icterina*		×	×	×	×	×	×	×		×	×
From East	*E. complanata*					×						×
From East	*A. c. cataracta*	×			×	×						×
From East	*A. couperiana*					×	×		×		×	×
From East	*E. lanceolata*		×			×				×		×
From West	*E. fraterna*				×	×						×
From West	*A. triangulata*					×						×

River from the Apalachicola River system: *Elliptio icterina*, which is abundant throughout the Apalachicolan region; *Elliptio fraterna*, which is dominant in the Choctawhatchee River system; and *Alasmidonta triangulata*, which seems to be more abundant in the Apalachicola than in the Savannah River. It probably cannot be determined whether the six species discussed moved from east to west, or from west to east, but their distribution by stream confluence is evident.

Two additional cases of stream capture are postulated: 1) The abundance of *Anodonta cataracta* in Uphauppee Creek of the Alabama-Coosa River system and its presence in Uchee Creek of the Apalachicola River system suggest the possibility of a former connection here, where *Anodonta cataracta*, *A. imbecilis*, *Elliptio arctata*, *Strophitus subvexus*, and *Anodontoides radiata* could also have passed from one river system to the other (Plate 1, C). 2) The presence of *Anodonta cataracta* in the Choctawhatchee River system and *Elliptio fraterna* in the Chattahoochee River system argues for a former commingling of the headwaters of the Choctaw-

TABLE 1, D. UNIONIDAE MOSTLY ENDEMIC TO THE APALACHICOLAN REGION AND PENINSULAR FLORIDA.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system	Peninsular Florida
V. villosa				×	×	×	×		×
A. peggyae			×	×	×	×			×
E. jayensis						×			×
M. walkeri				×	×	×			
P. pyriforme				×	×	×			
Q. infurcata				×	×	×			
L. subangulata				×	×				
E. sloatiana				×	×				
F. succissa	×	×	×						
P. strodeanum	×	×	×						
L. australis	×	×							
F. escambia	×	×							

Table 1, E. Unionidae endemic to individual river systems in the Apalachicolan region.

	Escambia River system	Yellow River system	Choctawhatchee River system	Apalachicola River system	Ochlockonee River system	Suwannee River system	St. Marys River system	Satilla River system
E. crassidens downiei								×
A. wrightiana					×			
L. binominatus				×				
E. nigella				×				
E. chipolaensis				×				
A. neisleri				×				
Q. burkei			×					
L. haddletoni			×					
L. jonesi			×					
V. choctawensis			×					
O. rotulata	×							

hatchee River with a tributary of the Chattahoochee River (Plate 1, D).

The unionid species that are endemic to the Apalachicolan region and Peninsular Florida show an orderly pattern of distribution (Table 1, D). While major stream confluences can be demonstrated, and minor ones only inferred, the analyses of Tables 1, A-D, argue convincingly, though heuristically, that the distribution of the Unionidae is not fortuitous, and that no method of dispersal other than the natural one need be postulated.

The great number of endemic species in individual river systems (Table 1, E) is evidence that this portion, at least, of the fauna is old, an observation made by Clench and Turner (1956: 104). The floodings of the coastal plain and lower upland country during the Pliocene and Pleistocene limited endemism to the larger river systems. Thus the lack of any endemic species in the Yellow River system (Table 1) is explained by inundation. It was subsequently repopulated by species from the Escambia and Choctawhatchee River systems.

CHAPTER 2

The distribution of the Unionidae in the Southern Atlantic Slope region as evidence of a former stream confluence of the headwaters of the Apalachicola and Savannah river systems.

The Atlantic Slope region defined and subdivided. This region consists of those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, and also including Newfoundland and Labrador, since, at least, *M. margaritifera* and *A. cataracta fragilis* persist north of the St. Lawrence. The area can be subdivided into a Southern and Northern region, since the unionid fauna consists of an assemblage of species of both southern and northern origin.

The Southern Atlantic Slope region extends from the Altamaha River system, Georgia, to the James River system, Virginia, for this is the last river system to the north with a clearly southern assemblage of species. *The Northern Atlantic Slope region*, as regarded here, begins with the York River system, since, with the probable exception of *E. lanceolata*, the remaining six species are all part of the northern fauna (see Table 2). As discussed previously, the St. Marys and Satilla river systems to the south of the Altamaha River system are regarded as part of the Apalachicolan region.

TABLE 2. DISTRIBUTION OF THE UNIONIDAE OF THE ATLANTIC SLOPE REGION FROM THE ALTAMAHA TO THE POTOMAC RIVER SYSTEMS, AND RELEVANT SPECIES FOUND IN THE APALACHICOLA RIVER SYSTEM.

Apalachicola River system		Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
	1. *Pleurobema collina* (Conrad)										×			×			
	2. *Pleurobema masoni* (Conrad)		×	×			×		×	×	×	×	×	×			
	3. *Elliptio spinosa* (Lea)	×															
	4. *Elliptio congaraea* (Lea)		×	×	×	×	×		×								
	5. *Elliptio waccamawensis* (Lea)							×									
	6. *Elliptio dariensis* (Lea)	×															
×	7. *Elliptio fraterna* (Lea)			×													
×	8. *Elliptio complanata* (Lightfoot)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
	9. *Elliptio hopetonensis* (Lea)	×															
×	10. *Elliptio icterina* (Conrad)	×	×	×	×	×	×	×	×								
×	11. *Elliptio arctata* (Conrad)			×		×			×								
×	12. *Elliptio lanceolata* (Lea)	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
	13. *Elliptio shepardiana* (Lea)	×															
×	14. *Uniomerus tetralasmus* (Say)	×	×	×	×	×	×	×	×	×	×	×	×				
	15. *Lasmigona subviridis* (Conrad)			×		×	×		×	×	×			×	×	×	×
	16. *Alasmidonta heterodon* (Lea)									×						×	×
	17. *Alasmidonta undulata* (Say)					×	×		×	×	×		×	×	×	×	×
×	18. *Alasmidonta triangulata* (Lea)		×	×		×											
	19. *Alasmidonta arcula* (Lea)	×															
	20. *Alasmidonta varicosa* (Lamarck)			×		×			×					×			×
×	21. *Anodonta cataracta cataracta* Say	×		×		×	×	×	×	×		×	×	×			×
	22. *Anodonta implicata* Say																×
	23. *Anodonta gibbosa* Say	×															
×	24. *Anodonta imbecilis* Say	×	×	×		×	×		×				×				
×	25. *Anodonta couperiana* Lea	×		×	×	×			×								
	26. *Strophitus undulatus* (Say)			×		×			×	×	×	×	×	×	×	×	×
	27. *Carunculina pulla* (Conrad)	×		×		×			×	×							
×	28. *Villosa vibex* (Conrad)	×	×	×	×	×	×	×	×	×							
	29. *Villosa delumbis* (Conrad)	×	×	×	×	×	×	×	×	×							
	30. *Villosa constricta* (Conrad)					×			×	×	×	×		×			
	31. *Ligumia nasuta* (Say)													×			×
	32. *Lampsilis cariosa* (Say)		×	×		×		×	×	×	×		×		×	×	×
	33. *Lampsilis dolabraeformis* (Lea)	×															
	34. *Lampsilis ovata* (Say)																×
	35. *Lampsilis ochracea* (Say)			×				×			×			×	×	×	×
	36. *Lampsilis radiata radiata* (Gmelin)						×				×	×					×
	37. *Lampsilis splendida* (Lea)	×	×	×		×											
11	TOTAL NUMBER OF SPECIES	18	12	21	8	20	13	9	19	14	12	8	9	12	7	8	14

Table 2, A. Unionidae, most of which are widely distributed in the Northern Atlantic Slope region, all but one of which terminate in the Southern Atlantic Slope region, but are of diverse origins.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
A. implicata																×
L. nasuta													×			×
A. heterodon									×						×	×
L. radiata radiata						×		×		×						×
A. undulata					×	×		×	×	×		×	×	×	×	×
S. undulatus			×		×			×	×	×	×	×	×	×	×	×
L. subviridis			×		×	×		×	×	×			×	×	×	×
A. varicosa			×		×			×					×			×
L. cariosa			×				×			×	×		×	×		×
L. ochracea		×	×		×		×	×	×	×		×		×		×

Analysis of the distribution of the species (Table 2). All of the species of Unionacea found in the Atlantic Slope region are covered in this paper except *Margaritifera margaritifera* (Linnaeus), whose southern terminus is in Pennsylvania, below the Wisconsin drift border;[1] *Alasmidonta marginata* (Say), which is restricted to the upper Susquehanna River, Pennsylvania; and *Anodonta cataracta fragilis* Lamarck from Nova Scotia and northward (figured by Athearn and Clarke, 1962: 28, pl. 2, figs. 3–4, and Clarke and Rick, 1963: 15). Forty species comprise the unionid fauna of the Atlantic Slope region, but one, *Lampsilis ovata* (Say), was artificially introduced from the west at the turn of the century (p. 387). Of the remaining thirty-nine species, sixteen occur in the Northern Atlantic Slope region. Twelve of these are also found in the Southern Atlantic Slope region. Of the twenty-three additional species found on the Southern Atlantic Slope, seven appear to have been derived from the west, nine are endemic to the region, and seven are endemic to individual river systems.

The Atlantic Slope unionid fauna is

[1] Flint (1957: 361) mentioned that along the Atlantic coast, the limit of the Nebraskan drift border extends somewhat farther south of the limit of the Wisconsin drift border (sometimes earlier referred to as the terminal moraine), but that it is ill defined.

Table 2, B. Unionidae thought to have originated on the Atlantic Slope, found in the Apalachicolan region, and which afford evidence of a former confluence of the Apalachicola and Savannah river systems.

	Apalachicola River system	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
E. complanata	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
E. lanceolata	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×
A. cataracta cataracta	×	×		×		×	×	×	×	×		×	×	×		×	×
A. couperiana	×	×		×		×			×								

TABLE 2, C. UNIONIDAE DERIVED FROM THE APALACHICOLAN REGION, FOUND IN THE SAVANNAH RIVER SYSTEM, WHICH AFFORD EVIDENCE OF A FORMER CONFLUENCE WITH THE APALACHICOLA RIVER SYSTEM, AND WHICH TERMINATE IN THE SOUTHERN ATLANTIC SLOPE REGION.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
U. tetralasmus	×	×	×	×	×	×	×	×	×	×	×	×				
A. imbecilis	×	×	×		×	×		×				×				
V. vibex	×	×	×	×	×	×	×	×								
E. icterina	×	×	×	×	×	×	×	×								
E. arctata			×		×			×								
A. triangulata		×	×		×											
E. fraterna			×													

distinct, consisting of species clearly derived from the fauna of the Interior Basin, and a secondary, or Atlantic (Simpson, 1900: 505), fauna also originally of Interior Basin origin, but whose ancestry is more remote. The Atlantic fauna consists of *Elliptio spinosa* (Lea), *Alasmidonta heterodon* (Lea), and *A. undulata* (Say). It may also include *A. triangulata* (Lea) and *Pleurobema collina* (Conrad).

All of these ten species (Table 2, A) are found in the Northern Atlantic Slope region. One of them, *Anodonta implicata*, is not found in the Southern Atlantic Slope region, whereas the remaining nine species terminate there. *A. implicata*, *Lampsilis*

TABLE 2, D. SUMMARY OF THE RELATIONSHIPS OF THE UNIONIDAE OF THE SAVANNAH RIVER SYSTEM. THE ARROWS IN THE FOLLOWING ILLUSTRATION INDICATE THE POSSIBLE DIRECTION OF MIGRATION.

Savannah River system		Apalachicola River system
1. *Pleurobema masoni* (Conrad)	←(1)	*Pleurobema pyriforme* (Lea)
2. *Elliptio congaraea* (Lea)	←(2)	*Elliptio fraterna* (Lea)
3. *Elliptio fraterna* (Lea)	←(3)	*Elliptio fraterna* (Lea)
4. *Elliptio complanata* (Lightfoot)	→(4)	*Elliptio complanata* (Lightfoot)
5. *Elliptio icterina* (Conrad)	←(5)	*Elliptio icterina* (Conrad)
6. *Elliptio arctata* (Conrad)	←(6)	*Elliptio arctata* (Conrad)
7. *Elliptio lanceolata* (Lea)	→(7)	*Elliptio lanceolata* (Lea)
8. *Uniomerus tetralasmus* (Say)	←(8)	*Uniomerus tetralasmus* (Say)
9. *Lasmigona subviridis* (Conrad)		
10. *Alasmidonta triangulata* (Lea)	←(9)	*Alasmidonta triangulata* (Lea)
11. *Alasmidonta varicosa* (Lamarck)		
12. *Anodonta c. cataracta* Say	→(10)	*Anodonta c. cataracta* Say
13. *Anodonta imbecilis* Say	←(11)	*Anodonta imbecilis* Say
14. *Anodonta couperiana* Lea	→(12)	*Anodonta couperiana* Say
15. *Strophitus undulatus* (Say)		
16. *Carunculina pulla* (Conrad)	←(13)	*Carunculina parva* (Barnes)
17. *Villosa vibex* (Conrad)	←(14)	*Villosa vibex* (Conrad)
18. *Villosa delumbis* (Conrad)	←(15)	*Villosa lienosa* (Conrad)
19. *Lampsilis cariosa* (Say)		
20. *Lampsilis ochracea* (Say)		
21. *Lampsilis splendida* (Lea)		

Table 2, E. Unionidae endemic, with an exception, to the Southern Atlantic Slope region.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system	Cape Fear River system	Neuse River system	Pamlico River system	Roanoke River system	Chowan River system	James River system	York River system	Rappahannock River system	Potomac River system
P. masoni		×	×			×		×	×	×	×	×	×			
V. constricta					×			×	×	×	×		×			
P. collina										×			×			
V. delumbis	×	×	×	×	×	×	×	×	×							
C. pulla	×		×		×			×	×							
E. congaraea		×	×	×	×	×		×								
L. splendida	×	×	×		×											
E. dariensis[1]	×															

[1] Also found in the St. Johns River system, Florida.

radiata, Alasmidonta varicosa, L. ochracea, and *L. cariosa* originated on the Northern Atlantic Slope. *Strophitus undulatus* and *Lasmigona subviridis* are thought to have crossed the divide of the Appalachian Mountains. *Ligumia nasuta* probably originated in the lake drainage of Ohio. *Alasmidonta heterodon* and *A. undulata* are probably relicts. The origin of these species are discussed in Chapter 3.

Elliptio complanata and *Anodonta cataracta* are found throughout the Northern Atlantic Slope Region, and probably originated there. *Elliptio lanceolata* extends only to the Susquehanna River system, Pennsylvania, and is thought to be of southern origin. All three of these species (Table 2, B) are discussed (in detail) in Chapter 3. *Anodonta couperiana* is abundant in Peninsular Florida, but since it does not appear to be present in the Suwanee and Withlacoochee river systems, it probably spread into the Apalachicolan region by stream confluence.

In the Apalachicolan region, *E. complanata* is found only within the Apalachicola River system, where it does not reach the size it does on the Atlantic Slope. *E. lanceolata* and *A. cataracta* are more widely distributed than *E. complanata;* but all three species are much less abundant there than they are on the Atlantic Slope.

Seven species of Unionidae (Table 2, C) entered the Southern Atlantic Slope region directly from a former confluence of the headwaters of the Apalachicola and Savannah river systems, and they all reach the limits of their distribution within this region.

Of the twenty-one species of Unionidae found in the Savannah River system, eleven species (Table 2, D) also occur in the Apalachicola River system, and another five were probably derived from Apalachicolan species. The remaining five species are clearly of Atlantic Slope origin.

Seven species of Unionidae are endemic to the Southern Atlantic Slope (Table 2, E) and one other extends into the Atlantic drainage of Peninsular Florida. The following possible species pairs, or analogs, are suggested:

Savannah River system	Apalachicola River system
P. masoni	*P. pyriforme*
E. congaraea	*E. fraterna* or *c. crassidens*
C. pulla	*C. parva*
V. delumbis	*V. lienosa*

Southern Atlantic Slope region	Southern Atlantic Slope region
P. collina	*P. masoni*
E. dariensis	*E. congaraea*
L. splendida	*L. radiata radiata*

Southern Atlantic Slope region	Tennessee River system
V. constricta[1]	*V. vanuxemensis*

[1] Discussed in Chapter 3, p. 280.

Table 2, F. Unionidae endemic to individual river systems of the Southern Atlantic Slope region.

	Altamaha River system	Ogeechee River system	Savannah River system	Edisto River system	Cooper-Santee River system	Pedee River system	Waccamaw River system
E. waccamawensis							×
E. spinosa	×						
E. hopetonensis	×						
E. shepardiana	×						
A. arcula	×						
A. gibbosa	×						
L. dolabraeformis	×						

Seven species of Unionidae are endemic to individual Atlantic Slope river systems (Table 2, F), six of them to the Altamaha. These are discussed below. The species pair *Elliptio waccamawensis—E. congaraea* is recognized.

It is suggested that the species in the left hand list evolved in some part of the Altamaha River system that must have been isolated for considerable time. Text-figure 3 shows that the Hazlehurst Terrace caused the Ocmulgee and Oconee rivers to be separated. This terrace was formerly thought to have been formed during the early Pleistocene, but has recently been dated as Upper Miocene (Alt and Brooks, 1965: 407). If this latter date is correct, this isolation probably bears little or no relevance to the present fauna. (See Table 2, G.)

CHAPTER 3

The Unionacea of the Northern Atlantic Slope region, with a discussion of the probable origin of some of the Atlantic Slope species.

The Northern Atlantic Slope region has already been defined as extending from the York River system, Virginia, to the lower St. Lawrence River system, Canada, and beyond to Newfoundland and Labrador. All of the thirteen species that repopulated the Northern Atlantic Slope at the end of the Pleistocene above the limit of Wisconsin drift (near the Pennsylvania-New York boundary) are found between the York River system and the drift border.

Analysis of the distribution of the species.

Sixteen species comprise the Unionacea of the Northern Atlantic Slope region (Table 3). Eight are considered to be of northern origin (Table 3, A); three are of southern origin; three crossed the divide of the Appalachian Mountains; one is of ancient origin from palearctic Europe; one is of rather recent western origin. Clearly western species found at certain areas of postglacial contact, such as upper New York State and Lake Champlain, but which have

Table 2, G. Relationships of some of the Unionidae of the Altamaha River system.

With the one exception noted above, all of the Unionidae that are endemic to individual river systems in the Southern Atlantic Slope occur in the Altamaha. The following relationships are suggested for some of the species that occur there.

Elliptio spinosa (Lea)	[Not closely related to any other recent species, probably a relict.]
Elliptio dariensis (Lea)	*Elliptio congaraea* (Lea) (Allopatric)
Elliptio hopetonensis (Lea)[1]	*Elliptio complanata* (Lightfoot) (Sympatric)
Elliptio shepardiana (Lea)	*Elliptio lanceolata* (Lea) (Sympatric)
Alasmidonta arcula (Lea)	*Alasmidonta triangulata* (Lea) (Allopatric)
Anodonta gibbosa Say	*Anodonta cataracta cataracta* Say (Sympatric)
Lampsilis dolabraeformis (Lea)	*Lampsilis cariosa* (Say) (Allopatric)
Lampsilis splendida (Lea)[2]	*Lampsilis radiata radiata* Gmelin (Allopatric)

[1] Also found in the St. Johns River system, Florida.
[2] Endemic to the Southern Atlantic Slope.

Table 3. The Unionacea of the Northern Atlantic Slope region.

1. *Margaritifera margaritifera* (Linnaeus)
2. *Elliptio complanata* (Lightfoot)
3. *Elliptio lanceolata* (Lea)
4. *Lasmigona subviridis* (Conrad)
5. *Alasmidonta undulata* (Say)
6. *Alasmidonta marginata* (Say)
7. *Alasmidonta varicosa* (Lamarck)
8. *Alasmidonta heterodon* (Lea)
9. *Anodonta cataracta cataracta* Say
10. *Anodonta cataracta fragilis* Lamarck
11. *Anodonta implicata* Say
12. *Strophitus undulatus* (Say)
13. *Ligumia nasuta* (Say)
14. *Lampsilis cariosa* (Say)
15. *Lampsilis ochracea* (Say)
16. *Lampsilis radiata radiata* (Gmelin)

not spread significantly into the region, are not discussed.

Ortmann (1906, and 1913a: 364) suggested that the ancestors of the Atlantic Slope Unionidae listed above, with the exception of *Elliptio complanata* (Table 3, A), migrated around the northern end of the Appalachian Mountains, in preglacial times, by way of the Eirigan River, which flowed in the direction of the present St. Lawrence River. There was no barrier to their dispersal southward because the base-leveled coastal plain then extended much farther seaward.

During glacial episodes of the Pleistocene, the species found on the eastern side of the mountains were effectively separated from those of the Interior Basin, and speciation took place among them, probably south of the limit of glacial drift, early in the period. Later some of these species spread into the Southern Atlantic Slope region where the coastal region was base-leveled. After the Pleistocene, this assemblage of species occupied most of the northern territory lost by its predecessors.

Ortmann (1913a: 361) was unaware of the complete distribution of *E. complanata* and suggested that it had its center of radiation somewhere on the Southern Atlantic Slope. Matteson (1948a: 131) indicated that the predecessor of *complanata* reached the Savannah River system from the Alabama-Coosa River system by stream capture. In Chapter 1 of this paper, a different order of stream capture is postulated. It appears that the Apalachicola and Savannah river systems were connected and separated before the Apalachicola and Alabama-Coosa were joined, judging from the distributional evidence afforded by the unionid fauna. The present distribution of *complanata* in the Apalachicolan region, as it is restricted to the Apalachicola River system, also indicates this order of stream capture. It was probably already a species before its ancestor, unidentified by Matteson, was supposed to have arrived on the Atlantic Slope. *E. complanata* is related to *dilatata* (figured by Ortmann, 1919: 95, pl. 8, fig. 2) of the Interior Basin. Both species enjoy a certain ubiquitousness within their areas of distribution. The history of *complanata* is, in short, probably similar to that of the other species discussed above.[1]

Table 3, A. Unionidae found in the Northern Atlantic Slope region with close affinities to species of the Interior Basin, believed to have come around the northern end of the Appalachian Mountains.

Interior Basin	Northern Atlantic Slope
E. dilatata	*E. complanata*
A. marginata	*A. varicosa*
A. grandis	*A. cataracta cataracta*
A. grandis	*A. cataracta fragilis*
A. grandis	*A. implicata*
L. ovata	*L. cariosa*
L. ovata	*L. ochracea*
L. radiata siliquoidea	*L. radiata radiata*

[1] Walker (1910: 131) suggested the same origin of *E. complanata* as that presented here. He further thought that *L. subrostrata* and *L. nasuta*, and *A. calceolus* (figured by Clarke and Berg, 1959: 29, fig. 30) and *A. heterodon* had similar relationships and the same origins as the species pairs discussed above. However, Ortmann's arguments as to their origins are thought to be more trenchant and are followed here.

Ortmann (1919: 109) called attention to the presence of *complanata* in the small tributaries of the West Branch of the Susquehanna River, Pennsylvania, close to the divide, and to *dilatata* in the Allegheny River drainage, but he did not suggest that *dilatata* entered the Atlantic Slope here and speciated. He did, however, suggest that *Strophitus undulatus* and *Alasmidonta marginata* entered the Atlantic Slope here. These species are discussed later.

The Margaritiferidae is represented on the Northern Atlantic Slope region by a single species, *Margaritifera margaritifera*. It is a special case because of its origin, but it is included here since its post-glacial history is similar to that of the other species discussed above.

There is good evidence that *M. margaritifera* (figured by Ortmann, 1919: 2, pl. 1, fig. 1) reached the Pacific region from Asia during the Miocene or early Pliocene when the two continents were connected by a North Pacific (Bering) bridge (Walker, 1910). Walker further speculated that this species separately reached the Atlantic Slope by an Atlantic bridge over Iceland and Greenland, probably at roughly the same time.[1]

In any event, *M. margaritifera* appears to have reached eastern North America before the Pleistocene, during which time its range was restricted. Ortmann (1913a: 378) found it in Pennsylvania just south of the limit of glacial drift and suggested that Pennsylvania was at least one refugium where *M. margaritifera* survived the Pleistocene Epoch. Its present distribution, from Pennsylvania to Newfoundland and Labrador, is the result of a reoccupation of territory. Besides differing anatomically, this species contrasts with the Unionidae in its ecological preferences, since it lives in cold water of high alkalinity.

Table 3, B. Unionidae found in the Atlantic Slope region which appear to have crossed the divide of the Allegheny Mountains, or are represented by allopatric species.

Interior Basin	Atlantic Slope region
L. subviridis	*L. subviridis*
V. vanuxemensis	*V. constricta*
Allegheny River drainage	Upper Susquehanna River drainage
A. marginata	*A. marginata*
S. undulatus	*S. undulatus*

Ortmann (1913a: 371) found *Lasmigona subviridis* to be the dominant species in the Greenbrier and New rivers of the Kanawha River system, which extends across the divide but drains on the western side of it. With the exception of this one western drainage, the species is limited to, and rather widely distributed on, the Atlantic Slope. He suggested that this species developed in the western mountain streams from *Lasmigona compressa* (Lea) (figured by Clarke and Berg, 1959: 31, fig. 29), with which it appears to be allopatric; though, at present, the range of *compressa* is not close to that of *subviridis*. It lives in small creeks where the best opportunities for fishes to cross from one river system to another develop. Ortmann thought that it spread into the Atlantic Slope region by way of stream capture with the upper James River, but it has since been reported from the Roanoke River system, permitting the assumption that it might have reached the Atlantic Slope by stream capture between the New and Roanoke rivers. (See p. 285.)

Villosa constricta is restricted to the Southern Atlantic Slope, between the upper Catawba River of the Cooper-Santee River system and the James River system. It is

[1] The North Pacific bridge is well established. Kurtén (1966: 4) believes there were three separate intermigrations by this route, one in the late Paleocene, another in the early Eocene, and a third at some time in the late Middle or beginning of the late Upper Eocene. He further suggests a North Atlantic connection including the British Isles, Iceland, and Greenland, in the late Paleocene and early Eocene.

very close to *Villosa vanuxemensis* (Lea), (for reference to a figure see Simpson 1914, 1: 165) which is found in the Holston River and elsewhere in the Tennessee River system. It is not obvious where the ancestor of *constricta* came from; it may have entered the Roanoke from the New River along with *L. subviridis*, if it can be assumed that *vanuxemensis* was more widely distributed in pre-glacial time.

Strophitus undulatus and *Alasmidonta marginata* crossed the divide in central Pennsylvania, in the vicinity of Cambria, Westmoreland, and Indiana counties, where the Susquehanna drainage of the east has largely encroached on the Allegheny River of the west, and where stream capture has taken place (Ortmann, 1913a: 368). *A. marginata* remained restricted to the upper Susquehanna River system, while S. *undulatus* spread throughout the Atlantic Slope region. Both of these species go into very small streams and, in general, avoid large rivers.

Ligumia nasuta is allopatric with *L. subrostrata* Say (for reference to a figure see Simpson, 1914, 1: 99) of the central and western part of the Interior Basin. It probably developed in the lake drainage of Ohio in postglacial time and spread eastward into the Hudson River, following a course along the baseleveled coastal plain. It reached the James River system in the south and the St. Lawrence River system, Canada, in the north (Ortmann 1913a: 379). This species has a preference for quiet water.

Elliptio lanceolata occurs in the Apalachicolan region and on the Atlantic Slope but there it extends only to the Susquehanna River system, Pennsylvania. The present distribution argues that this is a southern species, but its immediate ancestors or the area of its speciation is obscure.

Alasmidonta undulata and *Alasmidonta heterodon* appear to be relicts of a much older, westerly derived fauna, since they no longer closely resemble any of the members of the genus found in the Interior Basin, nor do they resemble one another. These two *Alasmidonta* appear to have long existed on the Southern Atlantic Slope, but are now widely distributed above the drift border.

CHAPTER 4

The generic affinities of the Unionacea of the Apalachicolan region, Peninsular Florida, and Southern and Northern Atlantic Slope regions.

Summary

Over forty genera of Unionidae occur in the Interior Basin, many of which are also found in the Alabama-Coosa River system. In the Apalachicolan region are fourteen genera that occur in the Interior Basin as well as in the Alabama-Coosa River system. An additional genus, *Glebula*, is limited to the Coastal regions. In the Apalachicolan region also occur *Margaritifera*, *Alasmidonta s. s.*, and *Quincuncina*. The latter is endemic. The six genera found in Peninsular Florida occur in both the Apalachicolan and Atlantic Slope regions but are probably derived mostly from the former.

Nine of the eleven genera of Unionidae found in the Southern Atlantic Slope region are found in the Apalachicolan region. The exceptions are *Lasmigona* and *Ligumia*. Four of the genera appear to be of southern origin, and the remainder have affinities with both the north and south. Only seven of these genera occur in the North Atlantic Slope region. This region is also occupied by *Margaritifera*, which does not occur on the Southern Atlantic Slope.

Ortmann (1913a: 323), speaking of the Unionidae that reached the Atlantic Slope around the northern end of the Appalachian Mountains, noticed the diminution of genera from the Interior Basin, and concluded that "the Allegheny Mountains formed an important barrier to the eastward distribution of the bulk of the western fauna." It is noted here that along the

Table 4, A. The genera of Unionacea in the Apalachicolan region.

Margaritifera[1]	*Anodontoides*
Fusconaia	*Strophitus*
Ambelma[2]	*Obovaria*[4]
Quincuncina	*Carunculina*
Pleurobema	*Villosa*
Elliptio	*Lampsilis*
Uniomerus	*Medionidus*
Alasmidonta[3]	*Glebula*
Anodonta	

[1] See note on p. 280.
[2] See note on p. 270.
[3] *Alasmidonta* is represented in the Alabama-Coosa River system by *A. mccordi* Athearn (1964: 134, pl. 9, figs. a, b).
[4] *Obovaria* is found in the Alabama-Coosa River system and is represented in the Apalachicolan region only in the Escambia River, the next system immediately east of the Alabama-Coosa River system.

southern coastal plain, where no such great barrier existed, there is a similar diminution of genera from west to east.

It can be seen in Table 1 that fifteen of the seventeen genera found in the Apalachicolan region (Table 4, A) occur in the Alabama-Coosa River system. The exceptions are *Margaritifera* (represented by *M. hembeli*, a relict), which is also found in one other drainage to the west, the Bayou Teche, Louisiana, and *Quincuncina*, which is endemic to the Apalachicolan region. Although *Alasmidonta* occurs in the Alabama-Coosa River system, it does not appear close to *Alasmidonta s. s.*, which is found only in the Apalachicolan and Atlantic Slope regions.

Peninsular Florida is considered to be the area south and east of the Suwannee River system and south of the St. Marys River system. (Both of these systems are included here in the Apalachicolan region.) In this area occur only six genera (Table 4, B) derived from the west and north-east.

Table 4, B. The genera and subgenera of Unionidae in Peninsular Florida.

Elliptio s.s.
Uniomerus
Anodonta s.s [Not represented in this area]
Utterbackia
Carunculina
Villosa
Lampsilis s.s

Table 4, C. The genera and subgenera of Unionidae in the Southern Atlantic Slope region.

Pleurobema s.s. [Not represented in this area]
Lexingtonia. Endemic to the Southern Atlantic Slope
Elliptio s.s.
Cauthyria. Endemic to the Altamaha River system
Uniomerus
Lasmigona s.s [Not represented in this area]
Platynaias
Alasmidonta s.s.
Prolasmidonta. Endemic to the entire Atlantic Slope
Decurambis
Anodonta s.s. [Not represented in this area]
Pyganodon
Utterbackia
Strophitus
Carunculina
Villosa
Ligumia
Lampsilis s.s.

Of the eleven genera (Table 4, C) found in the Southern Atlantic Slope region, nine are represented in the Apalachicolan region where there is a total of seventeen genera. *Strophitus*, *Lasmigona*, and *Ligumia* are clearly from the North. Of these, *Strophitus* alone is represented in the Apalachicolan region by *S. subvexus* (Conrad), which is endemic to the region.

Of clearly southern origin are *Uniomerus* and *Carunculina*. *Pleurobema* and *Villosa* are probably of southern origin. The genera *Elliptio*, *Alasmidonta*, *Anodonta*, and *Lampsilis* have affinities with both the southern and northern elements of the fauna.

Of the eleven genera (Table 4, D) found in the Southern Atlantic Slope region, seven occur in the Northern Atlantic Slope region, where there also occurs an additional genus of Unionacea, *Margaritifera*. These eight genera repopulated the entire Northern Atlantic Slope above the limit of glacial

Table 4, D. The genera and subgenera of Unionacea in the Northern Atlantic Slope region.

Margaritifera
Elliptio s.s
Lasmigona s.s
Platynaias
Alasmidonta s.s.
Prolasmidonta. Endemic to the Atlantic Slope region
Decurambis
Anodonta s.s. [Not represented in this area]
Pyganodon
Strophitus
Ligumia
Lampsilis s.s.

drift, with the exception of *Lasmigona*, which only reaches the Hudson River system, New York. One of these, *Ligumia*, appears to have entered from the west at the close of the Pleistocene. With this exception, the other genera were established below the limit of glacial drift before that period.

CHAPTER 5

The relationship of the geomorphology and topography of the Apalachicolan and Atlantic Slope regions to their unionid faunas.

The Appalachian Mountains have been an effective barrier to the spread of Unionacea from the Interior Basin to the coastal area since postcretaceous time (Ortmann, 1913a: 383), although the original Appalachian Mountains were formed much earlier in the Permian Period as the result of lateral pressure. They consisted of a number of parallel anticlines and synclines that ran in a northeast-southwestern direction. These folds were pressed against an old block of Archaic rocks, the present Piedmont Plateau, that lay to the east of them.

The highest elevation of these folds was in the south, and the divide was well to the east, close to the old Archaic land. The rivers followed the structure of the mountains, running first between the parallel ridges (anticlines) in the synclinal valleys, and finding their outlets in a northwesterly direction toward the Interior Basin. On the Atlantic side of the divide, shorter streams originated in the highest elevations and flowed east and southeast across the Archaic rocks. Rivers also formed on the tops of the anticlines, and anticlinal valleys developed, parallel to the synclinal ones. The uppermost rocks of the anticlines were largely hard sandstones of Carboniferous age, below which were softer shales and limestones of Devonian age or older. The synclinal rivers ran uniformly over the same hard sandstone, but the anticlinal rivers, primarily those on the highest elevations, were the first to cut through the sandstone, allowing the rivers access to the softer rocks below. In time, the anticlinal valleys became more excavated than the synclinal valleys. This process advanced farthest in the eastern section of the mountains, so that what was once the highest elevation became a deep valley.

By the Cretaceous Period, nearly all of the Appalachian area was peneplaned, with the exception of a chain of monadnocks between eastern Tennessee and North Carolina, and scattered hills in northern New England. (These unreduced areas form the modern Great Smoky Mountains and the summits of the White Mountains in New Hampshire. Elsewhere there are widespread remnants of the peneplane even on the crests of the highest present ridges.) The coastal plain was covered with a shallow sea that deposited a veneer of beds on the Archaic rocks. Because of certain characteristics of the patterns of some of the present streams, it is thought that this sea extended further inland than is now indicated by existing beds.

The relief of the present Appalachian Mountains is due almost wholly to a series of broad regional upwarps that occurred in the early Cenozoic Era, giving the present elevation both to the already extant

mountain structures and to the subsequent sculpture of this complex mass by erosion. The Appalachian Mountain system of eastern North America extends in a wide belt, more or less parallel to the coast line for more than 1600 miles from the Gulf Coastal Plain in central Alabama to the St. Lawrence River, Quebec. The mountains are divided from west to east into four provinces. 1) The Cumberland, or Appalachian Plateau, which extends from Alabama to New York and merges with the Allegheny Plateau. This western area has been peneplaned, but the soft rocks of pre-Carboniferous age have not been reached. 2) The Appalachian Valley and Ridges that reach from Alabama to New York. In the south, this province has a valley-like appearance, but in the north, it becomes the Allegheny Mountains. The eastern part of these were originally much higher. They are cut into by anticlinal streams, which have carved out broad limestone valleys, with high ridges of harder rock between them. Within the Allegheny Mountains, and parallel to them on the east, where there was once the highest elevation, there is now the exceptionally broad Great Allegheny Valley. 3) The Blue Ridge is the highest part of the Southern Appalachian Mountains and extends from northeastern Georgia across western South and North Carolina into southwestern Virginia. The Blue Ridge of the Central Appalachians extends from Central Virginia into Pennsylvania where it continues as South Mountain. It is the flank of an anticline, consisting largely of Archaic rocks. It is less elevated here than in the south. 4) The Piedmont Plateau (or Upland) goes from central Alabama to the Hudson River, New York.

To the east of these mountain provinces lies the Coastal Plain; this is a continuation of the Archaic granites of the Piedmont Plateau, over which are much younger Cretaceous and Tertiary deposits of sea-lain limestone and poorly consolidated sand and clay. Waterfalls are so numerous at the boundary between the Piedmont Plateau and the Coastal Plain that it is known as the Fall Line. During the Pleistocene, a number of changes in the level of the ocean left terraces on the Coastal Plain that will be discussed below.

The whole Appalachian Mountain system has also been divided from south to north into three regions. 1) *Southern.* Northeastern Georgia to the New or Kanawha River, Virginia, and West Virginia. 2) *Central.* New River to the Hudson River valley (covered here to the Potomac River system). 3) *Northern.* Hudson River valley to the lower St. Lawrence River. This adumbration of the complex history of the Appalachian Mountains, primarily of the area under study, is offered as background. The relevant details follow.

The main backbone of the present Appalachian Mountains extends continuously from the divide between the Toccoa and Coosawattee rivers in northeastern Georgia to northern Virginia, and is known as the Blue Ridge. From it the streams flow northwest, southeast, or east. It has been mentioned that the original divide was well to the east, as is the present divide, and that the eastern streams did, and do, have a steeper grade and a shorter, more direct route to the sea. Since they had, and have, more eroding power than the streams of the western drainage, they have encroached on it. There has also been a tendency of the rivers on the Atlantic Slope to capture streams between systems.

Evidence of stream capture. The southern extremity of the Blue Ridge is the watershed of a number of rivers. The Toccoa, the Little Tennessee, and the French Broad all flow into the Interior Basin. Of concern here are the two systems that originate on the southeast side of the mountains and that flow into the Gulf of Mexico; the Etowah River of the Alabama-Coosa River system, which flows westward around Pine Mountain, Georgia, into the Appalachian

Valley and then into the Gulf; the Chattahoochee River of the Apalachicola River system, which flows southwestward into the Gulf; and the Tugaloo River of the Savannah River system, which also heads in the mountains and flows southeast into the Atlantic Ocean. On the Piedmont Plateau, as can be seen in Text-figure 1, (see p. 268) all three of these rivers have tributaries that presently are separated by minor divides. Matteson (1948a: 131) suggested that confluence occurred among these streams during the late Tertiary. It may have been later, but in any event, the distribution of the Unionidae in the several river systems indicates that confluence did take place.

A number of other Atlantic Slope river systems, in addition to the Savannah, have their sources near or in the Blue Ridge. The Cooper-Santee River system, which drains some 15,000 square miles of central South Carolina, has three main tributaries, the Saluda, Broad, and Catawba, all of which originate close to the divide. The Pedee River system's main tributary, the Yadkin, begins in Watauga and Caldwell counties, North Carolina, near the divide. The Roanoke River system, which has the Dan River as a major tributary, forms in Patrick County, Virginia. The Roanoke itself commences in the eastern foothills of the Blue Ridge.

It is only in the southern Appalachians that streams that flow westward still have their sources near, or in, the Blue Ridge. The best example is the New River, which preserves its ancient course and cuts across the divide. According to Campbell (1896: 674) there is a good example of stream capture in the uppermost Roanoke River, Virginia (Plate 1).

The headwaters of the Roanoke's North Fork run first in a southwesterly direction in a valley that clearly continued to New River; but just north of Christiansburg, Montgomery County, Virginia, the North Fork makes a sharp bend, cuts through Paris Mountain, then flows eastward and northeastward. It is clear that the Roanoke River has captured here a tributary of the New River. The presence of *Lasmigona subviridis* and *Villosa constricta* in the Atlantic Slope region adds credence to the geomorphological evidence.

Beginning with the Roanoke, the succeeding river systems, the James, Potomac, and Susquehanna, all flow more directly east and each one cuts farther back into the mountains (Campbell, 1896: 675). Campbell also assumes that stream capture has taken place between the headwaters of the Roanoke and James river systems, an assumption which might explain the presence of *Villosa constricta* in both systems.

The Potomac River cuts across the mountains and has, in northeastern West Virginia, reached the Allegheny Plateau. It now drains a longitudinal synclinal valley. Campbell (1896) further states that in the mountains, the Potomac River robbed the James River of tributaries, and that the Susquehanna River of Pennsylvania encroached on the Potomac. However, these sequences of stream captures seem too ancient to be relevant to the present unionid fauna north of the James. Many of the Unionidae appear to have spread along the baseleveled coastal plain; this spreading is discussed below.

The Piedmont Plateau. In Alabama, the Piedmont Plateau is divided into two regions. 1. The Ashland Plateau, the highest division, is an area of crystalline rocks, diversified by ridges. It is the mountainous portion of the Piedmont and includes Cheaha Mountain, the highest point in the state. It is drained by portions of the Alabama-Coosa River system. 2. The Opelika Plateau is lower and is underlain by Archean rocks; it has no striking topographic features. It is drained by the tributaries of the Tallapoosa River of the Alabama-Coosa system, which lies adjacent to the northwest border of the Archaic

rocks, and by the Chattahoochee River, which forms the eastern boundary of the state. On the Opelika Plateau the rivers have cut valleys some 200 feet below the general surface. The region continues into Georgia as the Greenville Plateau, and is drained by longitudinal streams that flow southwestward and westward to the Gulf. The remaining portion of the Piedmont of Georgia to the north is drained by dendritic streams. Those rivers that originate in the Piedmont of Georgia include: the Flint of the Apalachicola system, which flows into the Gulf, and the Ocmulgee and Oconnee of the Altamaha system and the Ogeechee system, which both flow into the Atlantic. In South Carolina the rivers have their sources in the mountains or on the Coastal Plain. In North Carolina the Piedmont rivers include: the Cape Fear, Neuse, Pamlico, and Chowan systems; and in Virginia, the York and Rappahannock systems.

Ortmann (1913a: 340) observed, in the area he studied, that the great majority of Atlantic Slope Unionidae go up into the mountains (where the rivers may have reached Cretaceous limestone) and approach the headwaters without significant depauperation.

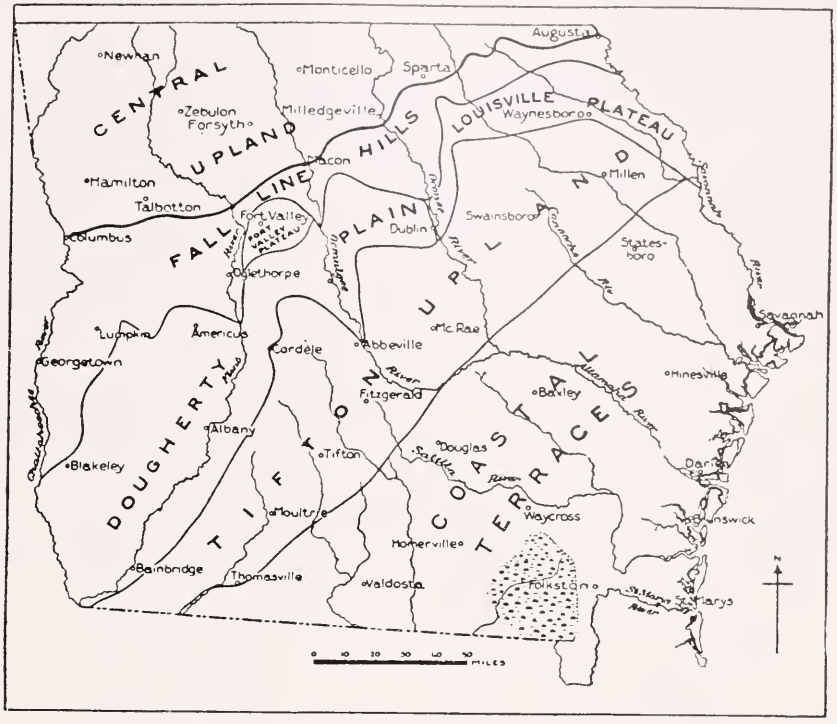
In the Apalachicola River system, present pollution prevents verification, but older records indicate that some of the unionid fauna of the Chattahoochee River extended on the Piedmont at least to the vicinity of Atlanta, Georgia. In the Flint River, which forms south of Atlanta, Unionidae are found in Line Creek, close to the headwaters.

On the Atlantic Slope of Georgia the unionid faunas of the major river systems —the Altamaha, Ogeechee, and Savannah —end abruptly at the Fall Line. The exceptions in the Altamaha River system are *Elliptio complanata* and *Anodonta c. cataracta,* which have been found near Stone Mountain, DeKalb County, the headwaters of the Ocmulgee River. In the Savannah River system the exceptions are *Elliptio complanata, E. congaraea,* and *Villosa delumbis,* which are found in the Broad River, opposite to which, in Abbeville County, South Carolina, have also been found *Pleurobema masoni, Elliptio fraterna, E. arctata, Lasmigona subviridis,* and *Lampsilis cariosa.*

The siliceous character of the Piedmont water, as illustrated in Text-figure 4, might offer an adequate explanation for the diminution of the fauna above the Fall Line. However, elsewhere on the Atlantic Slope siliceous water does not appear to be such an inhibiting factor to the distribution of the Piedmont Unionidae.

The Coastal Plain. The Coastal Plain is a continuation of the Archean rocks of the Piedmont over which occur Cretaceous and Tertiary deposits of sea-lain limestone and poorly consolidated sand and clay (Text-fig. 2). In spite of the apparent propinquity of the Apalachicola and Altamaha river systems in the Piedmont where the Chattahoochee passes close by the source of the Ocmulgee, the unionid fauna does not indicate any direct exchange of species. The Flint River has no large tributaries to the east, and in some places it is as much as fifteen miles from the divide that separates it from the drainage to the east, though Big Indian Creek, near Fort Valley, Houston County, a tributary of the Ocmulgee River, is only three miles distant. It would appear that the height of the Tifton Upland and Fort Valley Plateau, and the depth of the river channel on the Dougherty Plain, have prevented stream capture between these river systems for a long time.

During the Pleistocene the Coastal Plain was subjected to a number of invasions by the sea. According to Cooke (1945: 248), the maximum and earliest flooding left a record, the Brandywine Terrace [Hazlehurst in Georgia], which correlates with the Aftonian interglacial stage. The sea was thought to be 270 feet above the present level. As mentioned on p. 268, MacNeil cast doubt on the extent of Afonian flood-



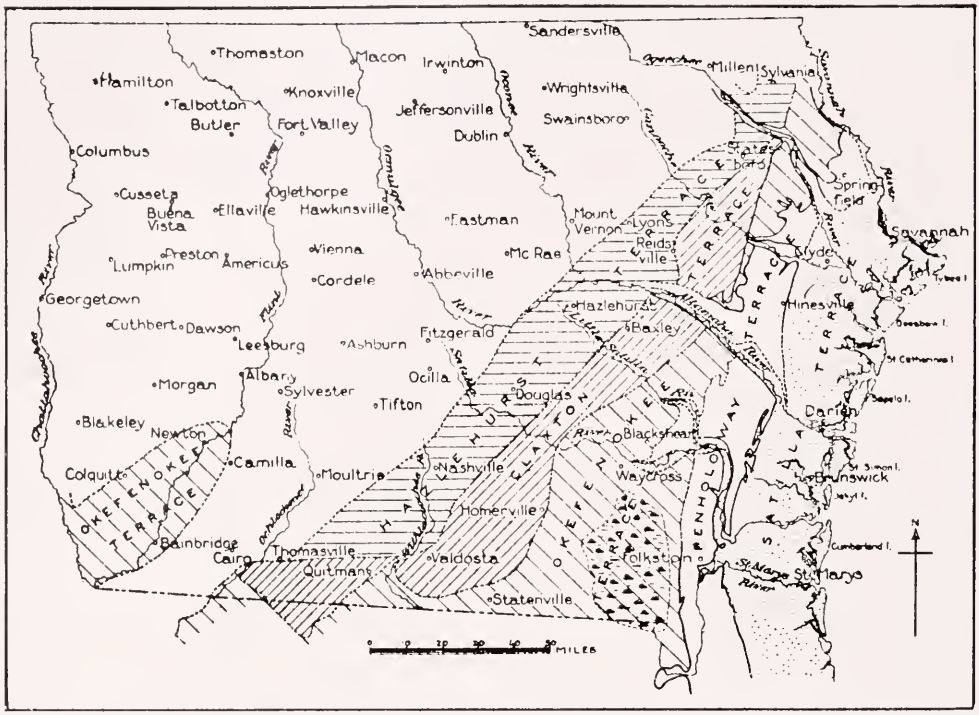
Text-figure 2. The topographic divisions of the Coastal Plain of Georgia. (From La Forge, 1925, fig. 2.)

ing, and concluded that there is no evidence to indicate that the sea ever reached a level more than 150 feet above the present one during the Yarmouth interglacial stage. He regarded the Brandywine Terrace to be of subaerial origin. Russell (1957: 427–428) suggested that the shore lines might have been subjected to differential uplifting.

Oaks and Coch (1963), on the basis of cores made in Virginia, postulated six cycles of the Pleistocene seas, with maximum heights of 45 feet above present levels. They disagreed with the theory of "terrace-stratigraphy" and disapproved of the nomenclature of the terraces, or shore lines.

Alt and Brooks (1965) also objected to the nomenclature of the shore line scarps and their associated terraces, since the implication is that they refer to independent physiographic units rather than to component parts of a single physiographic unit. In spite of these valid objections, some of the terrace names are well established in the literature and are retained here, but are used in the broader sense implied by Alt and Brooks.

On the basis of the geological evidence, Alt and Brooks (1965) concluded that the 215–250 [270] foot shore line was occupied during the Upper Miocene. This dating was confirmed by Laesse (1968) with botanical evidence. Alt and Brooks also concluded that the 90–100 foot shore line was occupied during the Pliocene. Alt (1968) further concluded that the 70–80 foot shore line also dated from the Pliocene. He recognized three Pleistocene shore lines: one at 40–45 feet, which he assigned to the Aftonian interglacial; a second at 25–30 feet, which he assigned to the longer Yarmouth interglacial; and a third at 5–10 feet, which he assigned to the Sangamon interglacial.

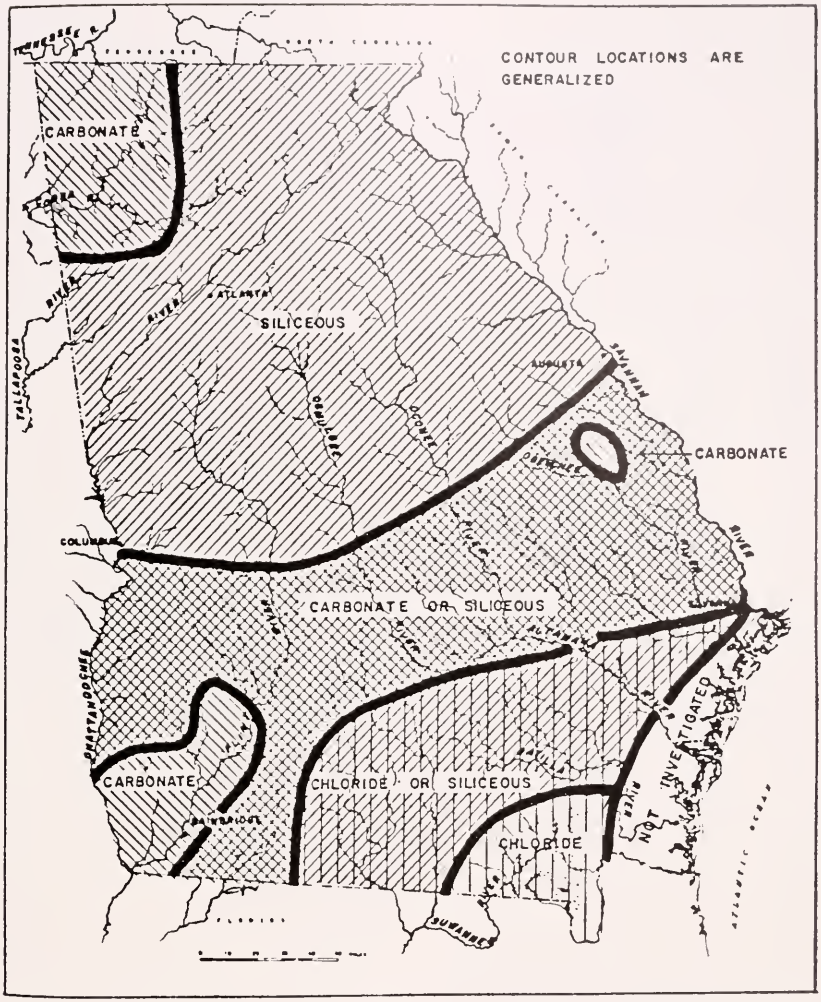


Text-figure 3. The Coastal Terraces on the Coastal Plain of Georgia. (From Cooke, 1925, pl. 10, fig. A.)

The coastal terraces of Georgia are shown in detail in Text-figure 3 because some are especially relevant. These terraces were formerly defined as sea bottom uncovered and converted into land by a drop in sea level, but Hoyt and Hails (1967) now regard these Georgia terraces as former lagoon salt marshes. The terraces are not entirely confined to the coastal region, since all of the larger rivers have terraces of their own. A river terrace may be defined as the old floor of a valley within which an inner valley has been cut by a stream when deepening its channel. Thus, river terraces are fossil flood plains.

The various coastal terraces (or shore lines) are correlated below from oldest (top) to youngest:

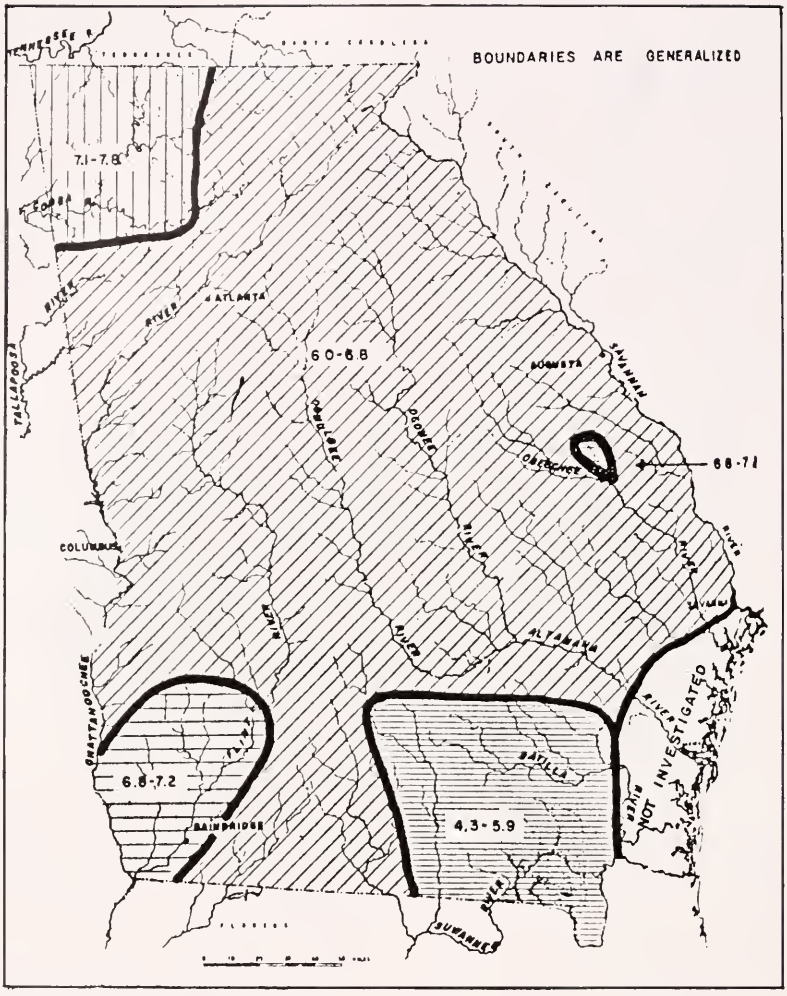
Murray (1961: 508)		Cooke (1925: 35)		MacNeil (1950: 99)	Alt and Brooks (1965) and Alt (1968)	
General maximum height		Georgia	Range	Florida	Time or Stage	
Brandywine	272 feet	Hazlehurst	270–215 feet		Upper Miocene	250–215 feet
Coharie	215 "	Claxton	215–160	Okefenokee	Pliocene	100– 90
Sunderland	170 "	Okefenokee	160–100			
Wicomico	100 "	Penholoway	100–60			
Penholoway	70 "	"		Wicomico	Late Pliocene	80– 70
Talbot	42 "	Satilla	60–0		Aftonian interglacial	50– 45
Pamlico	25 "	"		Pamlico	Yarmouth interglacial	30– 25
					Sangamon interglacial	10– 5



Text-figure 4. Water types of Georgia. (From Cherry, 1961, fig. 6.)

A number of the Coastal Plain rivers appear to have their sources above the level of maximum flooding by the sea; among these are the Escambia, Yellow, Choctawhatchee, Ochlockonee and Suwanee river systems in the Apalachicolan region and the Satilla and Edisto river systems on the Atlantic Slope. The Yellow, Satilla, and Edisto river systems appear to have been more effectively inundated by the sea, because their small unionid faunas suggest subsequent repopulation.

Among the river systems that are completely on that part of the coastal plain that was flooded during the Pliocene is the St. Marys. Text-figure 3 shows that it is entirely on the Okefenokee and Penholoway (Wicomico) formations. The river drains the Okefenokee Swamp, and its water, with a low *p*H, is high in chlorides or silicates (Text-figs. 4 and 5). Although the Satilla River is similar, it differs from the St. Marys in that a small portion of its headwaters is on the Tifton Upland, be-



Text-figure 5. Ranges in pH of Georgia water. (From Cherry, 1961, fig. 8.)

yond the area of maximum Pliocene and Pleistocene flooding. Both rivers have a small unionid fauna (Table 1). The dominant species in the St. Marys is *E. c. crassidens*, and in the Satilla, it is *E. crassidens downiei*. If the Satilla was a refugium, it is possible that *downiei* had a chance to evolve there and that *E. c. crassidens* came back from the west by a route not explained here.

The Waccamaw River system in South and North Carolina is of the same origin as the St. Marys. It is completely on the Wicomico and Chowan formations and has a typical coastal assemblage of Unionidae (Table 2), but it is remarkable in having an endemic species, *E. waccamawensis*.

Among the small river systems of more recent origin on the Coastal Plain in the Apalachicolan region in which Unionidae have been found are the Econfina and the Wasassasa. In the Econfina occur *Elliptio icterina*, *Villosa lienosa*, *V. vibex*, and

Lampsilis anodontoides. *E. icterina* occurs in the Wasassasa.

The systems of more recent origin on the Coastal Plain in the Atlantic Slope region are the Combahee, Ashley, Black, and White Oak rivers. The Combahee has five species: *E. complanata*, *E. icterina*, *Uniomerus tetralasmus*, *V. delumbis*, and *V. vibex*. In the other river systems occur either, or both, *E. complanata* and *icterina*, with the exception of the Black, in which *U. tetralasmus* also occurs.

It is generally regarded that the Pleistocene lasted for a million years, although Flint (1957: 301) states that, "all we can say with confidence is that the last major glaciation occurred within 30,000 years, and on the basis of sea floor stratigraphy, the Pleistocene as a whole, embraces at least 300,000 years, perhaps much more." In any event, during the Pleistocene at least five ice sheets pushed southward into the United States from centers of accumulation in Canada. The interglacial times are thought to have been of long duration with sea levels high. During the shorter glacial times the sea must have been relatively low, and the coastal plain often extended much farther to the east than it does at present.

Emery (1967) has convincingly shown that as early as 19,000 years ago (lowest level of the sea during the Wisconsin glacial stage) that this was so then.

Ortmann (1913a: 383) pointed out that there is a dispersal line directed both north and south on the Coastal Plain, because geophysical barriers have been largely removed by baseleveling. Lowland flooding allows fishes to migrate from one system to another. The present paucity of Unionidae in most of the coastal streams of recent origin indicates that dispersal was probably easier during one of the inter-glacial periods.

The importance of baseleveling and its faunal significance was well illustrated by Adams (1901).

CHAPTER 6

Summary and Conclusions

The Apalachicolan region as defined herein includes not only those river systems flowing into the Gulf of Mexico, from the Escambia to the Suwannee, but also the St. Marys and Satilla, which flow into the Atlantic Ocean. Forty-nine species comprise the unionid fauna of this region. Nineteen have affinities with species to the west or Interior Basin, twelve are endemic to the region, and eleven are restricted to individual river systems. Three species that were probably originally endemic to the region have spread into the Atlantic Slope region, and four others probably originated on the Atlantic slope.

The Atlantic Slope region is defined as those streams flowing into the Atlantic Ocean from the Altamaha River system, Georgia, to the lower St. Lawrence River system, Canada, including rivers in Newfoundland and Labrador. Since the area is occupied by an assemblage of species of both southern and northern origin, it can be divided into Southern and Northern regions. The former extends north to the James River system, Virginia, the northernmost system with a clearly southern assemblage of species. Forty species comprise the unionid fauna of the Atlantic Slope region, but one, *Lampsilis ovata* (Say), was artificially introduced from the west at the turn of the century. Of the remaining thirty-nine species, sixteen occur in the Northern Atlantic Slope region. Of the twenty-three additional species found on the Southern Atlantic Slope, seven appear to have been derived from the west, seven are endemic to the region, and seven are endemic to individual river systems. Two other species, thought to have originated on the Southern Atlantic Slope, are found in Peninsular Florida, and one of them has spread into the Apalachicolan region.

1. Because of their unique mode of distribution, the Unionidae are able to furnish

important evidence for past conditions of drainage by their present distribution, as was demonstrated by Ortmann (1913a: 381). The discontinuous distribution of the Unionidae of the Apalachicolan region indicates that there was once a confluence of the headwaters of the Alabama-Coosa and Apalachicola river systems. The presence of the same species and analogs in the Savannah River system on the Atlantic Slope as in the Apalachicola River also indicates confluence. The absence of some of the species found in both the Alabama-Coosa and Apalachicola river systems indicates that the confluence of the Apalachicola and Savannah river systems took place first. Two minor confluences are postulated: One between Uphauppee Creek of the Alabama-Coosa River system and Uchee Creek of the Apalachicola River system, the other between the headwaters of the Choctawhatchee River system and a tributary of the Chattahoochee River of the Apalachicola River system.

2. Contained in the fauna of the Apalachicolan region are species that are found in the Alabama-Coosa River system, having entered this system through a former confluence with it and the Tennessee River system. The region contains mainly endemic species of Interior Basin origin. A few species have reached it from the Atlantic Slope Region.

3. The presence of endemic species, primarily in the larger Apalachicolan river systems, indicates that these species had refugia above the maximum Pliocene and Pleistocene flooding, and originated before then.

4. Ortmann (1913a: 385) pointed out that the Allegheny Mountains formed an old and well-marked boundary between aquatic animals of the Interior Basin and those of the Atlantic Slope region since post-Cretaceous time. For the Unionidae this boundary includes the entire Appalachian Mountain system.

5. The Atlantic Slope unionid fauna is distinct, consisting of species clearly derived from the fauna of the Interior Basin, and a secondary, or Atlantic fauna (Simpson, 1900: 505), originally of Interior Basin origin, but whose ancestry is more remote.

6. In the Atlantic Slope region, most of the species that are clearly of Interior Basin origin are a northern group that migrated around the northern end of the Appalachian Mountains before the Pleistocene; there is also a southern group that entered the Atlantic Slope region through a confluence of the Apalachicola and Savannah river systems, also in pre-Pleistocene time.

7. The large number of endemic unionids in the Altamaha River system, Georgia, of both old Atlantic and Northern Atlantic Slope origin suggests that this system is particularly old and that it was sufficiently isolated during some of the Pleistocene to have facilitated speciation.

8. Dispersal in the Apalachicolan region appears to have been largely by stream capture. On the Atlantic Slope there is a dispersal line, directed both north and south, where barriers are rendered ineffective by baseleveling (Adams, 1901). The rate of dispersal was undoubtedly influenced by changes in sea level during the Pleistocene. Although it cannot be specifically demonstrated, stream confluence in the uplands also may have played a part in the dispersal of the Atlantic Slope species.

9. In the Appalachian Mountains, there are a few examples of species crossing the divide by stream capture. In addition to the confluence of the Apalachicola and Savannah River systems, there were confluences of the headwaters of the Roanoke and New rivers and of the Allegheny and Susquehanna river systems. Evidence of the former existence of these confluences is borne out by the present distribution of some unionid species in the adjoining systems and by the physiography.

10. *Margaritifera margaritifera* (Linnaeus), an ancient species from Europe,

had a refugium in Pennsylvania below maximum Pleistocene glaciation, and *Ligumia nasuta* (Say) appears to have migrated from the St. Lawrence Basin to the Atlantic Slope in postglacial time. These are two special cases of distribution.

PART II. A REVISION OF THE UNIONIDAE FROM THE ST. MARYS RIVER, FLORIDA, TO THE POTOMAC RIVER, MARYLAND.

INTRODUCTION

In spite of the parochial title of this section, I hold the belief, as do many evolutionary biologists, that most faunal studies are an anathema. Their authors seldom accurately determine subspecies (Mayr, et al., 1953: 181) and often even their determination of species is suspect. My excuse for this faunal approach is thought to be justified by the findings presented in Part I. I have studied the superfamily Unionacea for almost thirty years and each of the forty species covered in this section has been completely monographed, including those whose range extends beyond the area studied. Although the synonymy of each species is believed to be complete, and the modern species concept has been assiduously applied, infallibility of judgment is not claimed. If I am guilty of creating composite species, they will probably be found among the ubiquitous *Elliptio*. Nevertheless, if this is so, the postulations in Part I should not require serious modification since most of the species on which they are based are old and sufficiently discrete to satisfy a typologist.

History of the taxonomists and the collectors of the Atlantic Slope Unionacea.

The Taxonomists

Three species of Unionacea found in the Atlantic Slope region were figured in the first printed book devoted entirely to the study of mollusks. This was the great folio volume by Martin Lister, *Synopsis Methodicae Conchyliorum*, which appeared in London in 1685, at the close of the English Renaissance. This work was cited by Linnaeus in 1758 for *Margaritifera margaritifera;* by Lightfoot[1] in 1786 for *Elliptio complanata;* and by Gmelin in 1791 for *Lampsilis radiata radiata*. It was not until January of 1817, when volume two of Nicholson's *First American Edition of the British Encyclopedia* appeared, which included Thomas Say's article on Conchology, that many of the common Atlantic Slope Unionidae were described and figured. Eleven of Say's species are recognized here. Many of these were redescribed two years later, in 1819, by Lamarck in volume VI of his *Histoire Naturelle des Animaux sans Vertèbres*. Only three of his names are recognized in this paper. In 1830 and 1831 Isaac Lea of Philadelphia describe several new species from the Southern Atlantic Slope region, and in 1834 Timothy A. Conrad published a little volume, *New Fresh Water Shells of the United States*, which included many of the species he had found in the southeastern states.

A bitter battle arose between Lea and Conrad over the priority of some of the species, but their polemics, discussed by Wheeler (1935), are only of historical interest. Lea continued to describe Unionidae from the Southern Atlantic Slope until 1874, by which time he had burdened the literature concerning the few species found there with over one hundred and fifty names. In this paper, nine of Conrad's taxa and fifteen of Lea's are considered valid.

With the demise of Isaac Lea, the describing of the Unionidae of the southeastern states, exclusive of Florida, was

[1] See p. 314.

essentially over. Between the years 1883–1934, the Wrights, father and son, described fifty-two species of mollusks, most of which were from Florida (Johnson, 1967a). The Wrights were a pair of unsophisticated naturalists who redescribed many species, and aside from *Villosa villosa*, which is described in this paper, their other relevant taxa are included in the various synonymies.

The Collectors

The first serious student of fresh-water mollusks to make a collecting trip to South Carolina and Georgia was Timothy A. Conrad. His route of 1833 is shown in detail by Wheeler (1935: 26, 27). Before and after this time, most collections were made by interested local residents who sent their material to Isaac Lea, and occasionally to Conrad, for description. In the 1830's Lea received Unionidae from Lewis Leconte, J. H. Couper, Professor Shepard, and Edmund Ravenel.

These men made it possible for Lea to describe most of the endemic species in the Altamaha River, Georgia. Later, Dr. J. P. Barratt sent him shells from the Abbeville District of South Carolina. From the Carolina's Lea received, in his later years, shells from E. Emmons and especially from C. M. Wheatley.

No extensive collecting took place on the Southern Atlantic Slope after Lea's time, until W. J. Clench and P. Okkelberg made a trip to Georgia in 1929. This trip was followed by another by Clench and H. van der Schalie in 1932; and then by Clench, C. V. MaCoy, and H. D. Russell in 1934. The collections made in 1929 and 1932 were shared by the Museum of Comparative Zoology and the University Museum, University of Michigan. The remaining collections are in the Museum of Comparative Zoology. In 1937 van der Schalie made a survey of the mollusks of the Ogeechee River, Georgia, for the Museum of Zoology, University of Michigan. The last major expedition to the Southern Atlantic Slope of Georgia was made by W. J. Clench, K. J. Boss, and S. L. H. Fuller in 1962, for the Museum of Comparative Zoology. Since then, Ruth Patrick (1967) of the Academy of Natural Sciences of Philadelphia has had J. Bates and S. L. H. Fuller make collections of Unionidae in the Savannah and other Atlantic Slope river systems, in connection with her limnological studies.

In 1950–51 W. M. Walter made an extensive survey of the Neuse River system, North Carolina. This collection was divided among the Museum of Comparative Zoology, United States National Museum, and Museum of Zoology, University of Michigan.

In the Carolinas and northward, collecting has been adequate, but not organized in a way that can be discussed. Many stations have been made by casual collectors, and Ortmann collected systematically in Virginia.

THE PRIMARY SYSTEMATIC STUDIES OF APALACHICOLAN AND ATLANTIC SLOPE UNIONACEA.

Charles T. Simpson's *Notes on the Unionidae of Florida and the Southeastern States* (1892) was the first attempt at a revision of any of the species of the Southern Atlantic Slope region. This work was followed (1900) by his *Synopsis of the Naiades*, which was expanded into the *Descriptive Catalogue of the Naiades* (1914). These two works include a revision of the Naiades on a worldwide basis. Simpson's species concepts, in so far as they concern the Apalachicolan and Atlantic Slope regions, have been generally accepted, with but few changes, until recently. His were scholarly works. Simpson was among the more competent malacologists of his time. He included in his works almost every taxon relevant to the North American Unionacea that had appeared before 1914.

After Simpson's work, aside from some

studies by Ortmann, little was done on the Unionacea of the Apalachicolan region until van der Schalie wrote the *Naiad Fauna of the Chipola River, in Northwestern Florida* (1940). This was followed by Clench and Turner's *Freshwater Mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River* (1956). Further additions were made by Athearn in *Three new unionids from Alabama and Florida and a note on Lampsilis jonesi* (1964) and by Johnson in *Additions to the unionid fauna of the Gulf drainage of Alabama, Georgia and Florida* (1967b).

The Unionacea of the Northern Atlantic Slope region were elegantly monographed by Ortmann, who wrote the *Naiades of Pennsylvania*, pt. 3 (1919). Recently, Clarke and Berg (1959) made a modern study of the *Freshwater Mussels of Central New York* which complemented Ortmann's work to the north. This work was followed by the *Freshwater Mussels of Nova Scotia* by Athearn and Clarke (1962).

This brief review of the primary literature on the Unionacea of the Apalachicolan and Atlantic Slope regions itself explains the reason for carrying the present study to the Potomac River. To have carried it further would have been redundant, in view of the quality of the work of Ortmann, Clarke and Berg, and Athearn and Clarke.

Classification of the Unionacea

The classification based on the anatomy of the genera of Unionacea proposed by Ortmann (1911, 1912a) is used here. Since Ortmann's time a few necessary nomenclatural changes have been made, but no one has substantially modified his concepts of the evolution of the North American genera.

In 1927 Frierson, an ardent naturalist and an oldfashioned typologist, published *A Classified and Annotated Check List of the North American Naiades*. He stated his method and philosophy:

> "Many generic divisions have been proposed, based upon characters of diverse kinds, some being those of the hard parts, others those of the soft parts. These characters resemble each other in the respect that they all vary very much, and that none are constant. The general plan adopted herein is to select groups which may be typed by one member, the rest being evident kinfolk. Such new genera as are named herein are unaccompanied by diagnoses, a type shell being named, whose chief characters will forever give such diagnoses."

The paper is sprinkled with numerous generic and subgeneric names. It is not unfair to say that most of these names would have fallen into obscurity except for two events. In 1934, Thiele, in his *Handbuch der Systematischen Weichtierkunde* (2, pt. 3: 815–844), fell under both the systematic and taxonomic influence of Frierson. This is understandable, as he was a compiler, not a specialist in the Unionacea, and Frierson's work was the latest synthesis, and should have been the last word.

In 1942, 1949, and 1964, Modell, in *Das natürliche System der Najaden*, proposed that the relationships within the Unionacea can be found in the beak sculpture. He proposed forty-three new names for family groupings. He expected his system to be accepted on the basis of a few diagrammatic sketches of beak sculpture, and faith in a single character, which I have not found constant. Regarding the North American Unionacea he says:

> " . . . after Simpson's divisions were not sufficient for these purposes [i.e. questions concerning nomenclature]. I had to go along completely with the uniform system of Frierson in order to give a better picture. With this however I also had to use Frierson's concepts of Rafinesque's names completely."[1]

Of course, as mentioned before, the objection is to Frierson's systematics. His nomenclatural eccentricities, in the sense implied by Modell, are not of concern here.

[1] Translation by Stansbery and Soehngen, 1964, Sterkiana, no. 14, p. 18.

In short, it is not implied that Ortmann's anatomical system is perfect, only that it has not been improved on. Haas (1969a), in *Superfamilia Unionacea*, does not use Modell's system of classification for the higher categories. His species concepts of the North American Unionacea are those of Frierson (1927), with a few additions. In *Superfamily Unionacea* Haas (1969b) only discusses the genera.

SYSTEMATIC SECTION

The following abbreviations have been used in the text and on the plate captions.

ANSP—Academy of Natural Sciences of Philadelphia, Pennsylvania

MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts

MZUM—Museum of Zoology, University of Michigan, Ann Arbor, Michigan

USNM—United States National Museum, Washington, D. C.

Synonymy: For ease of reference, full citations are included for each taxon. Elsewhere in the text, references are abbreviated and require the use of the bibliography.

Isaac Lea often rushed brief Latin descriptions of his new species into print, a practice common in his time. These were subsequently followed by adequate descriptions and figures, which were then reprinted as "*Observations on the Genus Unio.*" Only page references to this work are included here since the plates and figures were never renumbered, but always kept the same numbers as in the preceeding reference. Lea generally gave several localities where each of his species had been found and did not select types, though he always figured a single specimen, for which he gave measurements. In lieu of the use of the word 'type,' under Article 73 (b) Int. Code Zool. Nomen. (1964), this is an "equivalent expression" and these specimens are regarded as holotypes. During the early part of the century, W. B. Marshall located most of these figured specimens in the United States National Museum. These have been rechecked, and their localities restricted when possible.

With but a few mentioned exceptions, all type localities were relocated, and are often rendered more specific from data on original labels and by references to standard atlases, modern county maps, or United States Geological Survey 1: 250,000 maps. These additional data are placed in square brackets.

Unless specifically mentioned to the contrary, all extant types have been examined and usually photographed. Almost none of Say's primary types have survived, and many of Conrad's are missing, whereas most of Lea's have been located.

Only pertinent references are included. Simpson (1914) is referred to only when our species concepts are similar or when the differences are easily reconcilable. The papers of Ortmann (1919), Clench and Turner (1956), Clarke and Berg (1959), and Athearn and Clarke (1962) are all referred to when relevant.

Descriptions: The measurements are only intended to convey the general size of specimens from a given station, or to illustrate sexual differences when they are relevant.

Anatomy and Breeding Season: These entries are included when such information is available. For widely distributed species, it should be borne in mind that the dates of the breeding season are not necessarily applicable to their entire range.

Habitat: Given when known:

Remarks: Statements made in this section, though applicable to each species over its entire range, are designed primarily to aid in differentiating one species from another within the Apalachicolan and Atlantic Slope regions.

Range: The ranges are intended to be all-inclusive for each species.

Records: The records, limited to the area of the study, are based mostly on speci-

mens in the major collections mentioned above under Abbreviations. All of these specimens have been examined, with a few noted exceptions. Sometimes similar records are found in several museums. If so, those in the Museum of Comparative Zoology are generally given preference. It is to be assumed that all records are in this museum, unless specifically mentioned to the contrary.

A few records from Virginia and Maryland, of common species, listed by Ortmann (1919) have not been reexamined, but are accepted with confidence. In each of these instances, references are given.

Walter (1956) did not list his data, but gave numbers on a figure of the Neuse River system. Because the first series of his collection is in the Museum of Comparative Zoology, his station numbers follow those of his localities which are included here. (See note on p. 323). The records of ubiquitous *Elliptio complanata* have been selected. They are more copious than is necessary to illustrate the distribution of the species, but they are an accurate index to the scope of collecting that has been done in the area covered in this portion of the paper.

In so far as possible, the records are arranged from headwaters to the mouth of the rivers, and from south to north, or west to east, as the case may be. Abbeville District, South Carolina, which occurs many times over in the records, includes the present counties of Abbeville and Greenwood, and most of McCormick.

Figures: When available, the holotypes are generally used to illustrate the various species. Often more than one illustration is included to show variability. Frequently, the data on the plate captions is not repeated elsewhere.

Key to the Unionidae Found Between the St. Marys River, Florida, and the Potomac River, Maryland.

The following key includes all of the species of Unionidae that are found between the St. Marys and the Potomac rivers, and it is designed to be used with specimens primarily from this area. The key in Clarke and Berg (1959: 13) may be used for the identification of the northeastern species of Unionacea. The key is artificial and is based on shell characters only. Some species of Unionidae are quite variable and some specimens may not key out correctly. Therefore it is advisable to confirm identifications made with the key by reference to the text and figures.

1. Hinge teeth completely absent. 4
   Articulating or vestigial hinge teeth present. 2
2. Hinge teeth vestigial. 3
   Articulating pseudocardinal teeth present. 8
3. Radial wrinkles on the posterior slope, each valve with one thin, depressed triangular pseudocardinal tooth; no lateral teeth ..... *Alasmidonta varicosa* p. 354
   Radial wrinkles absent on the posterior slope, each valve with a slight depression and then a slightly raised thickening just before the umbos ..... *Strophitus undulatus* p. 367
4. Umbos inflated, raised above the hinge line. 5
   Umbos flat, not raised above the hinge line. 7
5. Shell greatly inflated, especially toward the posterior ventral margin; Altamaha River system only ..... *Anodonta gibbosa* p. 359
   Shell somewhat inflated, but uniformly so. 6
6. Shell uniformly thin, nacre bluish white ..... *Anodonta cataracta cataracta* p. 356
   Shell prominently thickened along the anterior ventral margin below the pallial line; nacre salmon or copper colored ..... *Anodonta implicata* p. 360
7. Dorsal and ventral margins almost parallel; periostracum with broad green rays. Shell very thin and not much inflated ..... *Anodonta imbecilis* p. 362
   Ventral margin very broadly curved; periostracum with fine green rays. Shell very thin and not much inflated ..... *Anodonta couperiana* p. 365
8. Lateral teeth absent or vestigial. 9
   Articulating lateral teeth present. 11
9. Posterior ridge very rounded; shell elliptical or subrhomboid ..... *Alasmidonta undulata* p. 349
   Posterior ridge sharp; shell subtriangular. 10
10. Umbos anterior to the center, incurved; posterior slope acute ..... *Alasmidonta triangulata* p. 351
    Umbos centrally located, acutely incurved; posterior slope at almost 90° angle with

posterior ridge; Altamaha River system only ..... *Alasmidonta arcula* p. 352

11. Lateral teeth double in the right valve, single in the left one. Shell quite small ..... *Alasmidonta heterodon* p. 347
Lateral teeth single in the right valve, double in the left one. 12
12. Pseudocardinal teeth chunky and serrated, the more prominent one in the right valve not parallel to the hinge line. 13
Pseudocardinal teeth long and lamellate, with a tendency of the larger one in the right valve to be parallel to the hinge line. 29
13. Shell less than, or about, twice as long as high. 14
Shell distinctly more than twice as long as high. 37
14. Posterior ridge with faint ridges crossing lines of growth. 15
Posterior ridge without faint ridges crossing line of growth. 20
15. Shell subrhomboidal, subtriangular or quadrate, often solid, sometimes quite ponderous. 16
Shell subelliptical or elongated rhomboid, generally quite thin. 19
16. Posterior ridge of variable acuteness. 17
Posterior ridge sharp; shell rather thin, with green rays; Altamaha River system only ..... *Elliptio dariensis* p. 310
17. Shell ponderous, not rayed, or with thin dark green rays when young, generally blackish; St. Marys River system only ..... *Elliptio c. crassidens* p. 305
Shell not ponderous, with green rays of varying width, yellowish or chestnut ..... *Elliptio congaraea* p. 308
18. Posterior ridge sharp near the umbos, becoming faint and biangulate toward the posterior margin. Shell compressed, brownish. Young specimens occasionally with faint green rays ..... *Elliptio fraterna* p. 312
Posterior ridge consistently acute. Shell subinflated, brownish, often with narrow green rays over entire surface ..... *Elliptio waccamawensis* p. 313
19. Shell ponderous, inflated; posterior ridge double and of variable acuteness, brownish, rhomboid to obovate; Satilla River system only ..... *Elliptio c. downiei* p. 307
Shell not ponderous, disks flattened; posterior ridge double, but uniformly rounded. 20
20. Dorsal margin long, forming an acute angle with the obliquely descending posterior margin. 21
Dorsal margin very long, forming an extremely acute angle with the obliquely descending posterior margin, rendering the posterior end rather wedge shaped. 22
21. Shell rather uniformly trapezoidal, disk flattened; periostracum not usually shiny, often rayed, yellowish green to black ..... *Elliptio complanata* p. 314
Shell subrhomboidal, often somewhat pointed, very variable as to shape and degree of inflation; periostracum usually subshiny to shiny, often rayed, yellowish to brownish ..... *Elliptio icterina* p. 325
22. Valves with greatest degree of inflation at midpoint of posterior ridge; shell often rayed when young, becoming blackish with age. Periostracum smooth on the disk, rough toward the margins; Altamaha River system only *Elliptio hopetonensis* p. 324
Valves rather uniformly inflated; shell not rayed, occasionally greenish when young, becoming blackish with age. Periostracum generally distinctly satiny ..... *Uniomerus tetralasmus* p. 339
23. Shell small, not exceeding 65 mm in length, seldom rayed; periostracum yellowish, greenish, or brownish. Sexual dimorphism generally present. 24
Shell large, generally rayed, periostracum greenish yellow. Sexual dimorphism present. 28
24. Shell without spines on disk. 25
Shell with spines on disk. Outline subquadrate or subrhomboid; periostracum yellowish or brownish. Sexual differences not well marked ..... *Pleurobema collina* p. 300
25. Shell with a constriction of the ventral margin before a double, but faint, posterior ridge; periostracum smooth. 26
Shell with a regularly rounded ventral margin before a sharp double posterior ridge; periostracum with numerous heavy ridges. Outline of female long obovate; outline of male elliptical ..... *Carunculina pulla* p. 370
26. Outline subquadrate or rhomboid; periostracum often clothlike, blackish brown, occasionally with rays. Sexual difference not well marked ..... *Pleurobema masoni* p. 301
Outline of female short obovate; of male subelliptical. Periostracum yellowish green, with fine green rays over the entire surface ..... *Villosa constricta* p. 378
27. Outline a long ellipse; greenish rays over entire surface, periostracum satiny and clothlike ..... *Villosa villosa* p. 372
Shell not as above and much larger. 28
28. Posterior ridge well developed, especially toward the umbos. Shell subovate with narrow or wide rays generally distributed over a rather shiny yellowish background.

Sexual differences well marked in the shell ..... *Lampsilis ovata* p. 386
Posterior ridge low and rounded. Shell subelliptical, with wide rays generally distributed over a dull yellowish green background. Sexual differences not always well marked in the shell ..... *Lampsilis radiata radiata* p. 390

29. Left valve without a rudimentary interdental projection. 30
Left valve with a rudimentary projection, which fits into an interdental groove in the right valve; shell generally small, 45 to 65 mm in length, though giant specimens occur; subrhomboid, often with a low posterior wing when young ..... *Lasmigona subviridis* p. 343

30. Shell without spines on surface. 31
Shell with hollow spines in front of a sharp posterior ridge. Outline subtriangular; nacre purple. Altamaha River system only ..... *Elliptio spinosa* p. 303

31. Posterior ridge present and well defined, at least toward the umbos. Shell rather large and solid, yellowish, with varying amounts of the surface covered with green rays. Sexual dimorphism present. 32
Posterior ridge very broadly rounded. Shell small and thin, with numerous green rays over the entire surface, more greenish than yellow. 35

32. Surface of the shell either without rays or with some on posterior slope only. Periostracum shiny. 33
Surface of the shell with rays over the entire surface. Periostracum more often subshiny than shiny. 34

33. Posterior ridge low and rounded except toward the umbos, interdentum present. Nacre bluish white ..... *Lampsilis cariosa* p. 382
Posterior ridge very sharp, interdentum present; Altamaha River system only ..... *Lampsilis dolabraeformis* p. 384

34. Nacre bluish; rays narrow. Posterior ridge rounded except toward the umbos. Shell thin, no interdentum ..... *Lampsilis ochracea* p. 388

35. Periostracum shiny. 36
Periostracum distinctly satiny. ..... *Villosa villosa* p. 372

36. Narrow green rays, interrupted by growth rests ..... *Villosa delumbis* p. 375
Wide green rays, not interrupted by growth rests ..... *Villosa vibex* p. 373

37. Shell with ventral margin incurved, often sufficiently as to render entire shell arcuate. 38
Shell with ventral margin straight or curved, sometimes with a slight dorsal-ventral sulcus. Dorsal and ventral margins roughly parallel. 39

38. Shell somewhat over twice as long as high, subelliptical, posterior end produced; seldom rayed ..... *Elliptio arctata* p. 331
Shell over three times as long as high, trapezoidal, with the highest point at the anterior end tapering to a long point; rays visible when young. Altamaha River only ..... *Elliptio shepardiana* p. 338

39. Nacre silvery white; posterior end distinctly lance-head shaped; rays always present. Sexual dimorphism present. Females with a distinct postbasal swelling. ..... *Ligumia nasuta* p. 380
Nacre coppery or purple; dorsal and ventral margin almost parallel, often rayed, somewhat over twice as long as high ..... *Elliptio lanceolata* p. 333

Superfamily **Unionacea** Thiele 1935[1]

Family **Unionidae** (Fleming 1828) Ortmann 1911

Subfamily **Unioninae** (Swainson 1840) Ortmann 1910

Genus *Pleurobema* Rafinesque

Subgenus *Pleurobema s.s. Rafinesque*

Pleurobema Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 427. Species listed: *P. mytiloides* Rafinesque, *P. conica* ? Rafinesque [*nomina nuda*]. Rafinesque, 1820, Ann. Gén. des Sci. Phys. (Bruxelles), 5: 313. Species listed: *P. mytiloides* Rafinesque, *P. cuneata* Rafinesque.

Type species, *Unio mytiloides* Rafinesque. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 292.
Ortmann, 1912, Ann. Carnegie Mus., 8: 261. Ortmann and Walker (1922, Occ. Pap. Mus. Zool., Univ. Mich. no. 112, p. 20) state that the description of *P. mytiloides* in 1820 rendered the genus monotypic. This is not so, as the first use of *P. mytiloides* has no bearing on the subsequent recognition of the genus.

Under *Pleurobema s. s.*, Frierson (1927: 40–44) includes thirty-seven species and subspecies. It is probable that some of these taxa will be subsequently reduced to synonymy, but it is clear that this genus

[1] Or, Unionoidea (*oidea* is the standard ending for superfamily names, though *acea* has been generally used in molluscan taxonomy).

has achieved its greatest diversity in the Interior Basin.

Subgenus *Lexingtonia* Ortmann

Lexingtonia Ortmann 1914, Nautilus, 28: 28.
Type species, *Unio subplanus* Conrad. Original designation.

Ortmann instituted *Lexingtonia* as a genus because he believed that the six to eight subconcentric ridges of the beak sculpture and the red placentae differentiated it from *Elliptio* and *Pleurobema*. He mentions that the shell resembles *Fusconaia* in which all four gills serve as marsupia, but since he also says that only the outer gills are so used by *U. subplanus* Conrad = *masoni* Conrad, as in *Pleurobema,* the present author is placing *Lexingtonia* under *Pleurobema* as a subgenus, as did Frierson (1927: 44).

Under *Lexingtonia*, Frierson (1927: 44, 45) includes three species. Two of these are included here under the synonymy of *Pleurobema* (*Lexingtonia*) *masoni* (Conrad). The third, *Pleurobema utriculum* (Lea) belongs to the Tennessee River drainage. Its synonymy has not been reinvestigated, but it probably does not belong in this subgenus, which appears to be restricted to the Southern Atlantic Slope.

Pleurobema (*Lexingtonia*) *collina* (Conrad) Plate 2: 1–2

Unio collinus Conrad 1836, Monography Unionidae, no. 7, pl. 36, fig. 2 [plate caption only]. 1837, *op. cit.*, no. 8, p. 65 (North [= Maury] River, a branch of the James River [Rockbridge Co.], Virginia; type lot ANSP 20408 [lost]). 1840, *op. cit.*, no. 12, p. 109, pl. 60, fig. 3; this subsequently figured metatype, here selected, lectotype ANSP 41007.
Alasmidonta collina (Conrad). Simpson, 1914, Cat. Naiades, 1: 501.
Pleurobema collina (Conrad). Boss and Clench, 1967, Occ. Papers on Moll., 3: 45–51.

Description. Shell small, seldom reaching more than 55 mm in length. Outline subquadrate or subrhomboid. Valves subcompressed, subsolid. Anterior end regularly rounded; posterior end angular and slightly cut away below. Ventral margin straight or slightly arcuate centrally. Dorsal margin almost straight, terminating in a sharp angle with the obliquely truncated posterior margin. Hinge ligament short but prominent. Posterior ridge full, rounded, weakly biangulate toward the base of the shell. Umbos slightly elevated and located somewhat anterior to the middle of the shell, their sculpture consisting of three to four strong subconcentric ridges that form an indistinct rounded angle on the posterior ridge. Surface of the disk smooth, with undifferentiated concentric growth rings, surface sculptured with short differentiated bilateral spines especially in the region of the posterior dorsal slope and posterior quarter of the disk. Periostracum bright yellow or greenish yellow in young shells, becoming brownish in adults; rarely rayed with fine, narrow, broken, brownish lines.

Left valve with two ragged, triangular pseudocardinal teeth and two short, obliquely descending parallel lateral teeth. Right valve with one ragged, triangular pseudocardinal with a vestigial tooth above it; one lateral tooth. Beak cavities compressed; anterior adductor muscle scars deep, posterior ones very faint. Pallial line distinct, especially anteriorly. Nacre white, occasionally slightly pinkish, often bluish posteriorly.

Length mm	Height mm	Width mm	
55.0	34.7	20.3	Rivanna River, 2 mi. W Columbia, Fluvanna Co., Virginia.
46.0	30.0	19.0	North River [Rockbridge Co.], Virginia. Lectotype.

Anatomy. Discussed by Boss and Clench (1967: 47).

Breeding season. Probably tachytictic, releasing the glochidia during the summer. (Boss and Clench, 1967: 48.)

Habitat. Lives on sandy bottoms, in rather swift water.

Remarks. Pleurobema collina (Conrad) is a distinct Southern Atlantic Slope species. It is remarkable for the spines on the posterior slope of the valves. Usually the maximum number of pairs is three, and, in general, they are nearly bilaterally symmetrical. The first set of spines is about 3–4 mm from the umbo, the second 6–8 mm, and the third from 10–17 mm. The largest spines approach 5 mm in length and have a thickness of more than 1.5 mm. The spines are originally hollow, being closed ventrally at the end of their formation. (Boss and Clench, 1967: 47.)

Boss and Clench (1967) convincingly pointed out the similarity of *P. masoni* and *collina*. When the latter does not have spines, the two species can be easily confused, except that *masoni* is slightly more rhomboid and often has a brownish cloth-like periostracum, generally with at least a trace of green rays on the disk, whereas *collina* has a periostracum that is more yellowish and smooth, with only an occasional hint of brownish rays.

The range of this species was extended by Miss Carol Stein, who collected two small specimens in the Tar River in 1964.

Range. Southern Atlantic Slope: Tar River, of the Pamlico River system, North Carolina, and James River system, Virginia.

Specimens Examined

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pine Tops, Edgecombe Co. (Ohio State Museum).

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, Lexington; James River, near Natural Bridge (USNM), *all* Rockbridge Co. James River, Buchanan, Botetourt Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

Pleurobema (*Lexingtonia*) *masoni* (Conrad)

Plate 2: 3–10

Unio masoni Conrad 1834, New Fresh Water Shells United States, p. 34, pl. 5, fig. 2 (Savannah River, Augusta [Richmond Co.], Georgia; figured holotype ANSP 41333). Conrad, 1836, Monography Unionidae, no. 3, p. 28, pl. 12, fig. 2; figured paratype ANSP 41332.

Unio subplanus Conrad 1837, Monography Unionidae, no. 9, p. 73, pl. 41, fig. 1 ([North = Maury River, a] branch of the James River, Lexington, Rockbridge Co., Virginia; holotype ANSP 20412 [lost]).

Unio pumilus Lea 1838, Trans. Amer. Philos. Soc., 6: 23, pl. 7, fig. 17 (Black River [a tributary of the Neuse River] on the road to Fayetteville from Smithfield [= about 10 mi. W of Benson, Johnston Co.], North Carolina; figured holotype USNM 84545). Lea, 1838, Obs. Unio, 2: 23.

Unio merus Lea 1852, Trans. Amer. Philos. Soc., 10: 260, pl. 15, fig. 10 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85698). Lea, 1852, Obs. Unio, 5: 16.

Unio striatulus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 55, pl. 2, fig. 202; figured holotype USNM 84548. Lea, 1862, Obs. Unio, 8: 59.

Unio castus Lea 1860, Proc. Acad. Nat. Sci. Phila., 12: 306 (South Carolina). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 349, pl. 57, fig. 174; figured holotype USNM 84782. Lea, 1860, Obs. Unio, 8: 31.

Unio brimleyi S. H. Wright 1897, Nautilus, 10: 138 ([Walnut Creek of] Neuse River, Raleigh [Wake Co.], North Carolina; lectotype USNM 149651, selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 5, fig. 1. The type locality was restricted to Walnut Creek on the basis of Brimley's previously unpublished notes (Walter, 1956: 268).

Lexingtonia subplana (Conrad). Ortmann, 1914, Nautilus, 28: 29.

Description. Shell small, seldom reaching more than 50 mm in length. Outline subquadrate or rhomboid. Valves subcompressed, subsolid. Anterior end regularly rounded; posterior end angular and slightly cut away below. Ventral margin straight save for a slight undulation posteriorly. Dorsal margin straight, terminating in a sharp angle with the obliquely truncated posterior margin. Hinge ligament

short but prominent. Posterior ridge full, rounded, often with a second or tertiary ridge ending in slight biangulations toward the base of the shell. Umbos slightly elevated, located somewhat anterior to the middle of the shell, their sculpture consisting of six to eight rather crowded subconcentric ridges that form an indistinct rounded angle on the posterior ridge, in front of which they are wavy and corrugated. Disk often with irregular incremental striae, which sometimes render the periostracum rather clothlike; greenish, yellowish, or yellowish brown, sometimes with dark, dull greenish rays.

Left valve with two ragged, triangular pseudocardial teeth and two short, oblique descending, parallel lateral teeth. Right valve with one ragged, triangular pseudocardial with a vestigial tooth above it; one lateral tooth, which is sometimes double. Beak cavities compressed; anterior adductor muscle scars deep, posterior ones very faint. Pallial line distinct anteriorly only. Nacre white or bluish white, thinner and somewhat irridescent posteriorly.

Length mm	Height mm	Width mm	
62	41	22	Nottoway River, 3 mi. E Rawlings, Brunswick Co., Virginia.
47	28	19	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
31	21	14	Ogeechee River, Shoals, 12 mi. S Warrington, Warren Co., Georgia.

Anatomy. Discussed by Ortmann, 1914, Nautilus, 28: 29–30. "Glochidia semi-elliptical, without hooks. Length and height the same, 0.18 mm."

Breeding season. Ortmann found a gravid female in the North River, Lexington, Rockbridge Co., Virginia, on June 7, 1912.

Habitat. Lives on sandy bottoms, in rather swift water.

Remarks. Pleurobema masoni (Conrad) is a distinct Atlantic Slope species. It is closest to *P. pyriforme* (Lea) (figured by Clench and Turner, 1956: 162, pl. 8, fig. 6) which ranges from the Apalachicola to the Suwannee River system. The latter species is decidedly more subovate, with the posterior end tending to be broadly pointed. The ventral margin is rarely arcuate posteriorly; the disk is less compressed. The periostracum is often blackish or yellowish brown, but seldom rayed.

Except for examples of *P. masoni* from the Nottoway and James rivers, near the northern limit of its range, where the shells reach their maximum size and are found in relative abundance, this is a very rare species. In most drainage systems it is known from but a few examples. In 1961, Clench, Boss, and Fuller collected several thousand Unionidae in Georgia, but found only seven specimens of this species from two localities.

In the James River, Virginia, *P. masoni* is found closely associated with *P. collina*, under which see: *Remarks* on p. 301.

Range. Southern Atlantic Slope: Ogeechee River system, Georgia, north to the James River system, Virginia.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, 12 mi. SW Warrington, Warren Co. Buckhead Creek, 10 mi. SW Sardis, Burke Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM). *Georgia:* Broad River [Madison or Elbert Co.] (MZUM). Savannah River, Augusta, Richmond Co. (ANSP). Mill Race, 2 mi. N Sardis, Burke Co.

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Long Creek, Gaston Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (MZUM).

Cape Fear River System

Cape Fear River (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Hillsboro, Orange Co. Eno River, 6 mi. NNW Durham Center, Durham Co. (112). Walnut Creek, Raleigh (USNM); Neuse River, Raleigh; Little River, 2 mi. WSW Zebulon (6); *all* Wake Co. Black Creek [about 10 mi. W Benson, Johnston Co.] (USNM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. Tar River, Bruce, 9 mi. NW Greenville; Chicod Creek, 8 mi. W Greenville; *both* Pitt Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [=Maury] River, Lexington (ANSP); North River, above Buena Vista (Carnegie Mus.); [North River] Natural Bridge; *all* Rockbridge Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. James River, Richmond, Henrico Co. (MZUM).

Genus *Elliptio* Rafinesque

Subgenus *Canthyria* Swainson

Canthyria Swainson 1840, Treatise on Malacology, pp. 276, 378.

Type species, *Unio spinosus* Lea. Original designation.

Ortmann (1912, Ann. Carnegie Mus., 8: 269) suggests that "the spines [of the type] are unique, and would possibly justify the erection of a separate genus: *Canthyria*" for this species. Simpson (1914, 2: 704) states that the anatomy of *spinosa* is typical of *Unio* [=*Elliptio*]. Frierson (1927: 50) used this name as a genus to include both *spinosa* and *Pleurobema collina* (Conrad) on the basis of the spines. Boss and Clench (1967: 50) have clearly shown that these two species are of different lineages, and that the spines are a convergent character. In spite of the anatomical similarity to *Elliptio*, the shell morphology is not close to that of any other member of the genus. This appears to be a very old species, which is restricted to the Altamaha River system, Georgia.

This subgenus is monotypic.

Elliptio (*Canthyria*) *spinosa* (Lea)

Plate 2: 11

Unio spinosus Lea 1836, Description of a new *Unio*, pp. 1–4 (col. figs.) [not seen]. Lea, 1838, Trans. Amer. Philos. Soc., 6: 57, pl. 16, fig. 50 (Altamaha [River], Hopeton, near Darien [McIntosh Co.], Georgia; figured type in collection of Prof. Shepard [presumed lost]; Altamaha [River], Liberty [now Long] Co., Georgia). Lea, 1838, Obs. Unio, 2: 57. Simpson, 1914, Cat. Naiades, 2: 702.

Description. Shell medium to large, reaching 110 mm in length. Outline subrhomboidal or subtriangular. Valves subinflated to inflated, inequilateral, or almost equilateral; shell solid. Anterior end regularly rounded; posterior end slightly broader, ending in a point just below the medial line. Ventral margin slightly curved. Dorsal margin obliquely descending from the umbos, imperceptibly joining the descending posterior margin. Hinge ligament prominent, but short. Posterior ridge sharply angular, often with a faint secondary ridge above it, which renders the posterior slope slightly rugose. Umbos slightly elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several very tiny bars. Surface of the shell generally smooth and shiny with fine concentric sculpture.

Each valve ornamented with from one to five spines of various length (varying from 1–2.5 mm in length) straight or crooked, usually arranged in a row, roughly parallel to the posterior ridge. Periostracum greenish yellow or brownish in old shells, usually with faint greenish and yellowish rays.

Left valve with two pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one vestigial. Hinge line short and narrow, two obliquely descending straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one triangular and serrated, the more anterior one low and vestigial; one lateral tooth. Beak cavities moderately deep, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars well impressed. Pallial line distinct. Nacre pinkish or purplish, seldom white.

The spine is a tubular growth which appears to contain a lobe of the mantle until it has reached its full height, at which time the lobe fills the hollow spine with shell as it retreats.

Length mm	Height mm	Width mm	
110	54	48	Oconee River, 2.5 mi. N Glenwood, Montgomery Co., Georgia.
89	54	37	As above.
69	43	35	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 413). The anatomy is typical of *Unio* [=*Elliptio*] according to Simpson (1914, 2: 704).

Habitat. Lives buried from two to four inches deep in sand bars, in swift water.

Remarks. Elliptio spinosa (Lea) is known only from the Altamaha River system of Georgia. It is remarkable for the long spines that run parallel to the posterior ridge that are erected near growth rests during the first few years. None of the some sixty specimens seen have spines that are started after the shells had reached a height of about 30 mm. Presumably it is while the animal is young that the spines are most useful as grappling devices for holding the shells in sand.

Pleurobema collina (Conrad) of the Tar and James rivers of North Carolina and Virginia is also spined. This led Frierson (1927: 46) to unite the two species under the genus *Canthyria* Swainson 1840, but Boss and Clench (1967: 50) have clearly shown that the two species are of different lineages, and that the spines are a convergent character.

The distinct triangular shape; the equally distinctive greenish yellow, finely rayed, periostracum; the pink or purplish nacre; and the long spines distinguish *E. spinosa* from all other Atlantic Slope unionids.

In his "Travels of William Bartram," the well-known botanist mentions seeing this shell in 1773, probably near Frederica [Glynn Co., Georgia], but writing his journal from memory some thirteen years later, he claims to have seen it in the Mississippi River, Louisiana (Goodrich, 1930: 140).

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood, Montgomery Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. ENE Surrency, Appling Co. Altamaha River, 11 mi. N Odum; Altamaha River, 4 mi. NE Jesup; *both* Wayne Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Subgenus *Elliptio s.s.* Rafinesque

Elliptio Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 426 [*nomen nudum*]. Rafi-

nesque, 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 291. Species listed: *E. nigra* Rafinesque, *E. crassa* (Say), *E. viridis* Rafinesque, *E. fasciata* Rafinesque.

Type species, *Unio nigra* Rafinesque. Subsequent designation, Ortmann, 1912, Ann. Carnegie Mus., 8: 266. The previous use of *Unio crassidens* Lamarck as type species by Simpson (1900, Proc. U. S. Natl. Mus., 22: 700) is invalid since Lamarck's name was not included by Rafinesque in his list of species.

Eurynia Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris), 88: 426 [*nomen nudum*]. Rafinesque, 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 297. Species listed: *Unio dilatata. Unio latissima, Unio solenoides, all* Rafinesque.

Type species, *Unio dilatatus* [sic] Rafinesque. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 436.

Cunicula Swainson 1840, Treatise on Malacology, pp. 268, 378. Species listed: *C. planulata* Lea, *C. patula* Lea, *C. rubiginosa* Lea, *C. secura* Lea, *C. purpurascens* Lamarck.

Type species, *Unio purpurascens* Lamarck. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 335.
Ortmann and Walker (1922, Occ. Pap. Mus. Zool., Univ. Mich. no. 112, p. 28) selected *Elliptio* over *Eurynia* on the basis of page precedence.

Although *Elliptio* has been usually treated as a masculine noun, H. B. Baker (1964, Nautilus, 78: 33) has pointed out that Rafinesque consistently used *Elliptio* as feminine (e.g. *E. nigra*) and therefore the name should be thus treated.

Elliptio s. s. is represented by *Elliptio crassidens* (Lamarck) and *E. dilatata* (Rafinesque), (figured by: Ortmann, 1919: 95, pl. 8, fig. 2) in the Interior Basin, where they are widespread and locally abundant. At present, it is a moot question whether the several subgenera from Central America, included by Frierson (1927: 33–39) under *Elliptio,* belong there, but if they do, the evidence is that the area comprised of Mexico and Central America is one where considerable speciation has occurred in this genus.

Speciation within *Elliptio s. s.* has occurred primarily in the Apalachicolan region, Peninsular Florida, and the Southern Atlantic Slope region. In these regions the species of *Elliptio s. s.* are the most abundant Unionidae. *Elliptios* are often found in environments in which no other genera of Unionidae live, since some of them have an unusually wide environmental tolerance, even to silting and pollution. As a consequence, some of the species have developed many ecophenotypes, and at a given station there often appears to be less interspecific variation than infraspecific variation between localities. This variation has led to a plethora of names being applied to the several species.

Elliptio (*Elliptio*) *crassidens crassidens* (Lamarck)

Plate 3: 1–3

Unio crassidens var. b Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 71 (lac Erie [erroneous]; lectotype, Paris Museum, selected by Johnson, 1969, Nautilus, 83: 53, fig. 2, and the type locality restricted to the Ohio River, Cincinnati, Ohio). A composite species, restricted by Lea (1834, Proc. Amer. Philos. Soc., 5: 87), as first revisor, on the basis of his identification of the type = *Unio cuneatus* Barnes. See: Ortmann and Walker (1922: 28).

Unio nigra Rafinesque 1920, Ann. Gén. Sci. Phys. (Bruxelles), 5: 291, pl. 80, figs. 1–4 (Ohio River; type ANSP 20243, *teste,* Vannetta, 1915, Proc. Acad. Nat. Sci. Phila., 66: 555).

Unio cuneatus Barnes 1823, Amer. Jour. Sci., 6: 263 (Ohio River; type [lost]).

Unio incrassatus Lea 1840, Proc. Amer. Philos. Soc., 1: 268 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia). Lea, 1840, Trans. Amer. Philos. Soc., 8: 217, pl. 16, fig. 34; figured holotype USNM 84537). Lea, 1842, Obs. Unio, 3: 55.

Unio discus Sowerby 1868, *in* Reeve, Conch. Iconica 16, *Unio,* pl. 62, fig. 310 (India) *non* Lea 1838.

Unio lehmanii S. H. Wright 1897, Nautilus, 10: 138 (St. Marys River, [Nassau Co.], Florida; lectotype USNM 149650 selected by Johnson, 1967, Occ. Pap. Moll., 3: 7, pl. 6, fig. 3).

Unio danielsii B. H. Wright 1899, Nautilus, 13: 31 (Spring Creek [a branch of the Flint River], Decatur Co., Georgia; measured holotype USNM 168967, figured by Johnson, 1967, Occ. Pap. Moll., 3: 5, pl. 6, fig. 1).

Unio polymorphus B. H. Wright 1899, Nautilus, 13: 42 (Spanish Creek [a tributary of the St. Marys River, W of Folkston], Charleton Co., Georgia; lectotype USNM 152060 selected by

Johnson, 1967, Occ. Pap. Moll., 3: 8, pl. 6, fig. 2).

Elliptio pachyodon Pilsbry 1953, Pliocene Moll. Southern Florida, Acad. Nat. Sci. Phila., Monog. 8, p. 447, pl. 65, fig. 8 (St. Petersburg [Hillsboro Co.], Florida; type ANSP 18586; Pliocene).

Elliptio niger Rafinesque. Ortmann 1919, Mem. Carnegie Mus., 8: 91, pl. 8, fig. 1.

Elliptio crassidens incrassatus (Lea). Clench and Turner, 1956, Bull. Florida State Mus., 1: 171, pl. 8, fig. 1.

Description. Shell often large, exceeding 130 mm in length, though usually not exceeding 100 mm in the Atlantic drainage. Outline subrhomboid, or quadrate, somewhat produced posteriorly in older specimens. Valves somewhat inflated, rather solid to ponderous, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded and either somewhat pointed or biangulate. Ventral margin straight or slightly curved, sometimes arcuate in matures. Dorsal margin broadly rounded, usually indistinctly joining the obliquely descending posterior margin. Hinge ligament prominent, located posteriorly. Posterior ridge generally sharp and angular, especially when young, often becoming more broadly rounded with age. Posterior ridge generally double. Secondary ridge varying greatly as to prominence and distance from the primary ridge. This variation causes a considerable range as to degree of terminal biangulation, and further causes the posterior slope to vary from subtruncated to broad. Posterior slope generally with a few wrinkles radiating from posterior ridge to dorsal margin. Umbos rather full, but rather low, located in anterior third of shell, their sculpture consisting of a few coarse ridges running parallel to growth lines. Young shells may be rather smooth on the disk, developing concentric striae with age; posterior slope usually becoming more wrinkled. Periostracum fine when young, reddish brown or chestnut, sometimes yellowish with greenish rays; posterior slope generally darker. In older specimens, periostracum generally uniformly black. Left valve with two heavy, rough pseudocardinal teeth, the more anterior one smaller and lower. Hinge line rather short and broad, with two short, slightly curved lateral teeth. Right valve with one chunky serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars very deep, posterior ones and pallial line distinct. Nacre usually purplish, salmon, sometimes yellowish, posteriorly iridescent.

Length mm	Height mm	Width mm	
94	57	38	Spanish Creek, Charleton Co., Georgia.
71	40	28	As above.
62	40	30	As above.
54	36	23	As above.

Anatomy. Discussed by Lea (1863: 45).

Habitat. Lives in sandbars in large rivers and creeks in swift water.

Remarks. Elliptio c. crassidens (Lamarck) is a variable species throughout the Interior Basin, Alabama-Coosa River system, and Apalachicolan region. In the latter region, Simpson (1914, 2: 608) regarded *U. incrassatus* Lea as a variety, though he stated that, "A number of intermediate specimens from the Tennessee and Coosa rivers seem to connect the two completely." Clench and Turner (1956: 173), following Simpson, considered *incrassatus* a subspecies, but they also said, "Though the two extremes are distinct, there are all degrees of intergradation between the two forms [i.e. *crassidens* and *incrassatus*]." It is true that specimens from the Apalachicolan region are not usually as large as those from the Interior Basin, but smaller examples from both areas tend to have the characteristic radial wrinkles that extend from the posterior ridge to the posterior margin. Throughout the distribution of *E. c. crassidens*, there is a marked variation in the acuteness of the posterior ridge, the prominence of the secondary ridge and

concomitant posterior biangulation, and the breadth or acuteness of the posterior slope. There is a general tendency for the posterior ridge to be rounded and the posterior slope to be broad in specimens from the Apalachicolan region.

E. c. crassidens can be confused with some allopatric species in the Southern Atlantic Slope region, but in general, the thickness of the shell, the large, rough, pseudocardinals, and short hinge line, distinguish it from other species of *Elliptio*.

Range. Interior Basin: Mississippi drainage generally. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Amite River, Louisiana, east to the St. Marys River system, Florida. Replaced by *Elliptio fraterna* (Lea) in the Choctawhatchee River system and missing from the Ochlockonee and Suwannee river systems. Peninsular Florida: St. Petersburg, Hillsborough Co. (Pliocene).

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, 2 mi. E St. George; Spanish Creek, W Folkston; St. Marys River, 4 mi. SSE Folkston; *all* Charleton Co.

Elliptio (*Elliptio*) *crassidens downiei* (Lea)

Plate 4: 1–4

Unio downici Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 166 (Buck Lake, a bayou of the Satilla River, Wayne [Brantly] Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 210, pl. 25, fig. 91; figured holotype USNM 84854. Lea, 1859, Obs. Unio, 7: 28.

Unio satillaensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 166 (Satilla River, Camden Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 216, pl. 27, fig. 96; figured holotype USNM 84855. Lea, 1859, Obs. Unio, 7: 34.

Unio spissus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Satilla River, Wayne Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 208, pl. 25, fig. 89; figured holotype USNM 84853. Lea, 1859, Obs. Unio, 7: 26.

Description. Shell large, reaching up to 100 mm in length. Outline obovate, subobovate, or rhomboid. Valves rather inflated, solid, inequilateral. Anterior end regularly rounded; posterior end broadly rounded, slightly biangulate, or truncate. Ventral margin straight or curved, sometimes rendered arcuate by slight postbasal swelling. Dorsal margin broadly rounded, forming a slight angle, occasionally a very sharp one, with the obliquely descending posterior margin. Posterior ridge varies from being rather sharp to almost imperceptible. Secondary ridge usually present. Posterior slope subtruncated to broad. Umbos rather full, but low, located in anterior fifth of shell, their sculpture consisting of a few coarse ridges running parallel to growth lines. Periostracum fine when young, yellowish or brownish with green rays, becoming dull brown or chestnut with age, varies from being clothlike to smooth and shiny.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one somewhat triangular. Hinge line short and broad, with two short, slightly curved lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars very deep, posterior ones and pallial line distinct. Nacre purplish or flesh-colored, rather dull.

Length mm	Height mm	Width mm	
95	57	42	Satilla River, 3 mi. S Hortense, Brantly Co., Georgia.
84	49	36	Buck Lake, a bayou of the Satilla River, Brantly Co., Georgia. Holotype of *U. downiei* Lea.
76	57	40	Satilla River, Wayne Co., Georgia. Holotype of *U. spissus* Lea.

Habitat. Lives in sand in swift water.

Remarks. Elliptio crassidens downiei (Lea) is quite distinct from the highly variable typical form, and has a pattern of

variability of its own, even though occasional individuals are found that are very close to some specimens from the nearby St. Marys River system. Found only in the Satilla River, *downiei* is usually considerably more inflated than the typical form. There is a tendency for the shells from the upper reaches of the river to be obovate or elongate with the posterior ridge almost imperceptible and the posterior slope very broad. Some individuals are also sometimes slightly swollen in the postbasal region. In the lower part of the river, the shells, in general, become more rhomboidal, the posterior margin appearing truncate with the posterior ridge angular and the posterior slope sharp. The posterior slope of *downiei* lacks the radial wrinkles usually present in *E. c. crassidens;* the periostracum with its satiny clothlike, or even shiny appearance, and yellowish brown to chestnut color is also distinctive.

Range. Apalachicolan region: restricted to the Satilla River system, Georgia.

Specimens Examined

Satilla River System

Satilla River Drainage. *Georgia*: Satilla River, Wayne Co. Buck Lake, a bayou of the Satilla River; Satilla River, 3 mi. S Hortense; *both* Brantly Co. Satilla River, Camden Co.

Elliptio (*Elliptio*) *congaraea* (Lea)

Plate 5: 1–8

Unio congaraeus Lea 1831, Trans. Amer. Philos. Soc., 4: 72, pl. 6, fig. 4 (Congaree River, South Carolina; figured holotype USNM 85693). Lea, 1834, Obs. Unio, 1: 82.

Unio fulvus Lea 1834, Trans. Amer. Philos. Soc., 5: 96, pl. 13, fig. 39 (South Carolina; figured holotype USNM 85679). Lea, 1834, Obs. Unio, 1: 208.

Unio lecontianus Lea 1838, Trans. Amer. Philos. Soc., 6: 40, pl. 12, fig. 35 (Canoochee River, Liberty Co., Georgia; figured holotype USNM 84852). Lea, 1838, Obs. Unio, 2: 40.

Unio planilateris Conrad 1838, Monography Unionidae, no. 11 [back cover] (Black Water River, Virginia; Neuse River; Yadkin River; *both* North Carolina). 1840, *op. cit.*, no. 12, p. 103, pl. 57, fig. 1; type from Yadkin River, not in ANSP [lost]. The specimens from the additional localities were probably *Elliptio complanata* (Lightfoot).

Unio pusillus Lea 1840, Proc. Acad. Nat. Sci. Phila., 1: 286 (Ogeechee River, Liberty Co., Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 220, pl. 18, fig. 36; figured holotype USNM 85241. Lea, 1842, Obs. Unio, 3: 58.

Unio sordidis Lea 1852, Trans. Amer. Philos. Soc., 10: 254, pl. 12, fig. 1 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85688). Lea, 1852, Obs. Unio, 5: 10.

Unio gibbesianus Lea 1852, Trans. Amer. Philos. Soc., 10: 254, pl. 12, fig. 2 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85685). Lea, 1852, Obs. Unio, 5: 10.

Unio rufusculus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 258, pl. 14, fig. 7; figured holotype USNM 85683. Lea, 1852, Obs. Unio, 5: 14.

Unio forbesianus Lea 1852, Proc. Amer. Philos. Soc., 5: 251 (Savannah River, Georgia). Lea, 1852, Trans. Amer. Philos. Soc., 10: 264, pl. 16, fig. 17; figured holotype USNM 84542. Lea, 1852, Obs. Unio, 5: 20.

Unio buxeus Lea 1852, Trans. Amer. Philos. Soc., 10: 261, pl. 15, fig. 13 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85153). Lea, 1852, Obs. Unio, 5: 17.

Unio moussonianus Lea 1852, Trans. Amer. Philos. Soc., 10: 268, pl. 18, fig. 22 (Georgia; figured holotype USNM 85168). Lea, 1852, Obs. Unio, 5: 24.

Unio corvus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Buckhead Creek, Burke Co.; Ogeechee River; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 217, pl. 27, fig. 97; figured holotype USNM 84539, from Buckhead Creek. Lea, 1859, Obs. Unio, 7: 35.

Unio vestitus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 393 (Ogeechee River [Georgia]). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 189, pl. 25, fig. 259; figured holotype USNM 85332. Lea, 1862, Obs. Unio, 9: 11.

Unio dorsatus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 160 (Catawba River, North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila.,

ser. 2, 6: 300, pl. 45, fig. 112; figured holotype USNM 84494. Lea, 1869, Obs. Unio, 12: 60.
Unio strumosus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Yadkin River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 57, pl. 19, fig. 55; figured holotype USNM 85755. Lea, 1874, Obs. Unio, 13: 61.

Description. Shell medium to large, reaching up to 100 mm in length. Outline long, rhomboid, subrhomboid, sometimes almost subtriangular. Valves flat to subinflated, thin to solid, inequilateral. Anterior end regularly rounded; posterior end broadly rounded, slightly biangulate or truncate. Ventral margin straight or slightly curved, occasionally a bit arcuate. Dorsal margin short to very short, forming an indistinct angle with the obliquely descending posterior margin. Posterior ridge occasionally rather sharp but more often faint to imperceptible, with the slightest hint of a secondary ridge above. Posterior slope rather broad to very broad, with numerous fine ridges that radiate from the upper posterior ridge to the dorsal margin. Umbos rather full, but low, located in the anterior third to fourth of the shell, their sculpture consisting of a few coarse ridges that run parallel to the growth lines. Periostracum smooth when young, yellowish with fine to broad green rays, sometimes becoming yellowish green but more often light brown or chestnut, generally smooth on the disk, but roughened toward the margins.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one slightly smaller and a little lower. Hinge line rather short and broad, with two short, slightly curved, granular lateral teeth, the uppermost one sometimes very short and vestigial. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre generally white, occasionally light pinkish or purplish.

Length mm	Height mm	Width mm	
80	48	29	Savannah River, 7 mi. NE Newington, Screven Co., Georgia.
77	40	30	As above.
70	39	24	Briar Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co., Georgia.
51	30	18	As above.

Habitat. Lives in sand, in swift water.

Remarks. Elliptio congaraea (Lea) differs from *E. c. crassidens* of the Apalachicolan region in that the shell is less ponderous, with a tendency to be more rhomboid or subtriangular. It has a posterior ridge that is less sharp, and a broader posterior slope that is often biangulate. In some environments the posterior ridge merges imperceptibly into the posterior slope.

E. congaraea differs from *E. dariensis* (Lea). The latter has a much sharper posterior ridge, the posterior slope is more acute, with heavier sculpture, and is, in general, less often biangulate. *E. congaraea* differs from *E. crassidens downiei.* The latter is, in general, much more sharply rhomboidal and inflated.

Shells of *E. congaraea* from the Canoochee River are generally rather heavy and somewhat swollen, the posterior ridge faint and biangulate, the periostracum usually brownish yellow to chestnut and not rayed. Examples from the upper Ogeechee River tend to be moderately heavy and flat, the posterior ridge rather strong, but the preponderant form in the Ogeechee River is rather long with a faint broad biangulate posterior ridge. Shells from the Savannah River are inclined to be subtriangular with a rather sharp posterior ridge and acute posterior slope, but specimens from the tributaries tend to resemble the shells from the Ogeechee with their faint, broadly biangulate posterior ridge. The rivers to the north of the Savannah abound in the weak-ridged forms, and are often light brown or yellowish with more prominent green rays.

Range. Southern Atlantic Slope: Ogeechee River system, Georgia, north to the Cape Fear River system, North Carolina.

Specimens Examined

Ogeechee River System

Canoochee River Drainage. *Georgia*: Canoochee River, Bulloch Co. Canoochee River, Liberty Co. (USNM). Canoochee River, E Pembroke (ANSP); Canoochee River, near Clyde (MZUM); *both* Bryan Co.

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, 12 mi. SW Warrington, Warren Co. Ogeechee River, 4 mi. SW Mitchell, Glascock Co. Ogeechee River, 2 mi. S Louisville, Jefferson Co. Rocky Creek, 5 mi. SW Waynesboro, Burke Co. Ogeechee River, Scarboro; Ogeechee River, bridge, 1 mi. S Dover; Ogeechee River, 1.5 mi. SW Oliver; *all* Screven Co. (*all* MZUM). Ogeechee River, bridge, 1 mi. E Blitchton; Ogeechee River, Jinks Bridge, Route 16; Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke; Dolly Lake, about 1.5 mi. below Kiterlighter Camp; *all* Bryan Co. (*all* MZUM).

Savannah River System

Broad River Drainage. *Georgia*: Broad River, Huguenot, Elbert Co. (USNM).

Savannah River Drainage. *Georgia*: Savannah River, Elbert Co. Savannah River, Augusta; Spirit Creek, De Bruce; *both* Richmond Co. *South Carolina*: Savannah River, 6 mi. W Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, King Jaw Point, 10 mi. WSW Allendale (MZUM); *all* Allendale Co. *Georgia*: Brier Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co. Savannah River, 7 mi. NE Newington, Screven Co. *South Carolina*: Mouth of Vermezobre Creek (Savannah River Wildlife Res.) (MZUM); Savannah River at Governor Hamilton's [Mansion, 8 mi. S Hardeeville] (ANSP); *both* Jasper Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Edisto River, Givhans Ferry, 2 mi. NW Givhans, Dorchester Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina*: Congaree River.

Wateree River Drainage. *North Carolina*: Catawba River, Tuckasaga Ford [not found] (ANSP). *South Carolina*: Wateree River, Camden, Kershaw Co. (MZUM).

Pedee River System

Yadkin River Drainage. *South Carolina*: Yadkin River (ANSP, USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina*: Cape Fear River.

Elliptio (*Elliptio*) *dariensis* (Lea)

Plate 6: 1–4

Unio dariensis Lea 1842, Trans. Amer. Philos. Soc., 8: 246, pl. 26, fig. 61 ([Altamaha River] near Darien [McIntosh Co.], Georgia; figured holotype USNM 85691). Lea, 1842, Obs. Unio, 3: 84.

Unio monroensis Lea 1843, Descriptions Twelve Uniones. (Lake Monroe, Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 279, pl. 41, fig. 8; figured holotype USNM 85169. Lea, 1848, Obs. Unio, 4: 37.

Unio websterii B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 113, pl. 2, fig. 2 (Lake Woodruff, Volusia Co., Florida; lectotype USNM 125697, selected by Johnson, 1967, Occ. Pap. Moll., 3: 10, pl. 7, fig. 2).

Unio hartwrightii B. H. Wright 1896, Nautilus, 9: 121, pl. 2, figs. 4–6 (Lake Beresford [Volusia Co.], Florida; holotype USNM 151031, figured by Johnson, 1967, Occ. Pap. Moll., 3: 6, pl. 7, fig. 1 and the type locality further restricted on the basis of the original label to: [St. Johns River], Blue Springs [3 mi. S Lake Beresford, Volusia Co.], Florida).

Description. Shell often large, exceeding 130 mm in length. Outline subrhomboid or subtrapezoidal. Valves rather flat to subinflated, thin but strong, inequilateral. Anterior end regularly rounded; posterior

end occasionally a bit produced and slightly biangulate, but more often obliquely truncated. Ventral margin straight or slightly curved. Dorsal margin straight, forming a sharp angle with the obliquely descending posterior margin. Posterior ridge usually very sharp with a faint secondary ridge above. Posterior slope rather broad, but well defined, with numerous wrinkles on it. Umbos full to inflated, but rather low, located in the anterior third of the shell, their sculpture consisting of five or six double-looped bars, slightly more elevated and angular behind the sinus. Periostracum smooth when young, yellowish with fine green rays, becoming darker greenish yellow, or dark chestnut or blackish, generally smooth on the disk but sometimes roughened, especially on the posterior slope.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one slightly smaller and a little lower. Hinge line rather short and broad, with two short, slightly curved, granular, lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre generally purple, sometimes white, occasionally yellow.

Length mm	Height mm	Width mm	
130	77	47	House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co., Georgia.
98	58	35	As above.
78	55	28	[Altamaha River], near Darien [McIntosh Co.], Georgia.
41	23	14	House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co., Georgia.

Anatomy. Discussed by Lea (1863: 404).

Habitat. Lives in sand bars, in fast-flowing or even sluggish water.

Remarks. Elliptio dariensis (Lea) is restricted to the St. Johns River system, Florida, and the Altamaha River system, Georgia, and is close to *Elliptio c. crassidens* (Lamarck), but the shell of *dariensis* is never as ponderous; the posterior ridge is consistently much sharper, especially in immature individuals, and the posterior slope, though generally wrinkled, does not have the strong radial pattern typical of *E. c. crassidens.* Throughout its range, *dariensis* is more compressed than *E. c. downiei* (Lea) even when the posterior ridge of some individuals of both are not very acute.

Elliptio dariensis is also close to *E. congaraea* (Lea), which is found in the Ogeechee River, Georgia, to the Cape Fear River, North Carolina, but *congaraea* is more variable. It is often more rhomboid than *dariensis.* In *congaraea* the posterior ridge is less sharp, and more prone to be biangulate, resembling some examples of *E. crassidens downiei,* though the latter are more inflated. Immatures of *dariensis* tend to have a somewhat chestnut periostracum with subtle green rays, whereas *congaraea* is often quite yellow with rather bright green rays.

In the Altamaha River system, the largest specimens of *E. dariensis* are found in the lower Altamaha River. Older specimens have been confused with *E. hopetonensis* (which replaces *E. complanata* (Lightfoot) in the main river), but *hopetonensis* is proportionally longer and narrower, is without the sharp posterior ridge, and has no trace of sculpture on the posterior slope. Whereas *E. hopetonensis* is very common in the Altamaha River, *E. dariensis* is not. In a collection made by Clench, Boss and Fuller, 10 mi. NE Surrency, Appling Co., Georgia, several hundred *hopetonensis* were collected, but only three *dariensis.*

The especially sharp posterior ridge and relatively thin shell, and the similarity of the periostracum, especially as exhibited in

immatures, suggest that the forms described from the St. Johns River system are *E. dariensis*, even though the St. Johns and Altamaha river systems are separated by the St. Marys and Satilla river systems, which are inhabited by *E. c. crassidens* and *E. crassidens downiei* respectively.

Range. Peninsular Florida. St. Johns River system, Florida. Southern Atlantic Slope: Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Bozzy Branch, 4 mi. S Macon; Tobesofkee Creek, 5 mi. S Macon; *both* Bibb Co. Tucsowhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. Dicksons Creek, 10 mi. NE Fitzgerald, Ben Hill Co. Ocmulgee River, 1.5 mi. S Jacksonville; Ocmulgee River, below Lumber City, (H. D. Athearn); *both* Telfair Co.

Ohoopee River Drainage. *Georgia*: Little Ohoopee River, 1 mi. E Kite, Johnson Co. Little Ohoopee River, 11 mi. W Swainsboro; Ohoopee River, 1 mi. E Adrian; Ohoopee River, 0.5 mi. S Norristown; *all* Emanuel Co. Ohoopee River, above Reidsville, Tattnall Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, Long Co. Altamaha River, near Darien, McIntosh Co.

Elliptio (*Elliptio*) *fraterna* (Lea)

Plate 7: 1–5

Unio fraternus Lea 1852, Trans. Amer. Philos. Soc., 10: 263, pl. 16, fig. 15 ([Chattahoochee River] Columbus [Muscogee Co.], Georgia; paratype USNM 85398; Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85396). Lea, Obs. Unio, 5: 19.

Unio anthonyi Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 41 (Florida). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 197, pl. 27, fig. 266; figured holotype USNM 84986. Lea, 1863, Obs. Unio, 9: 19.

Elliptio mcmichaeli Clench and Turner 1956, Bull. Florida State Mus., 1: 170, pl. 7, figs. 1–2 (Choctawhatchee River, 8 mi. W Miller Cross Roads, Holmes Co., Florida; holotype MCZ 191922).

Description. Shell medium to large, reaching 100 mm in length. Outline subelliptical. Valves flat, rather thin but solid, inequilateral. Anterior end regularly rounded; posterior end somewhat produced and biangulate. Ventral margin rather uniformly straight. Dorsal margin straight or slightly curved, forming an angle with the obliquely descending posterior margin. Posterior ridge fairly well defined near the umbos, becoming faint toward the posterior margin, with a second faint ridge above, ending in a slight biangulation. Posterior slope slightly concave and broad, often sculptured toward the umbos with wrinkles that radiate from the posterior ridge to the dorsal margin. Umbos full but low, located in the anterior fourth of the shell. Periostracum smooth and shiny on the disk, light brownish, reddish brown, or yellowish, often with fine green rays when young, becoming uniformly brownish with age.

Left valve with two heavy, rough pseudocardinal teeth, the more anterior one smaller and lower. Hinge line very short and rather narrow; two rather long slightly curved lateral teeth. Right valve with one chunky, serrated pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones and pallial line distinct. Nacre usually white, sometimes pale pink to salmon, or purplish, especially toward the edges, iridescent posteriorly.

Length mm	Height mm	Width mm	
65	30	20	Abbeville District, South Carolina.
60	31	16	As above. Holotype of *U. fraternus* Lea.
50	27	17	As above.

Anatomy. Discussed by Lea (1863: 410).

Habitat. Lives in sand bars in large rivers and their smaller tributaries, in swift water.

Remarks. Elliptio fraterna (Lea) of the Choctawhatchee River system replaces the widely distributed *E. c. crassidens* (Lamarck) which is found in both river systems adjacent to the Choctawhatchee. It is obviously close to *crassidens*, but the shell of *fraterna* is lighter, the outline is subelliptical, and the shell is consistently more elongated and compressed. The posterior ridge is less acute and the posterior slope is broader. In the Atlantic drainage, *fraterna* resembles some forms of *E. crassidens downiei* and *E. congaraea*, but the shell of *fraterna* is consistently thinner and more compressed.

The discontinuous distribution of populations of *fraterna* was used as a reason for establishing *mcmichaeli* by Clench and Turner (1956: 171). In the United States National Museum are specimens from the Chattahoochee River, Columbus, Muscogee Co., Georgia. This locality is near the headwaters of the Choctawhatchee River system, and it is likely that *fraterna* spread into the Chattahoochee River in this vicinity, as is suggested here in Chapter 1. Further, commingling of the waters of the upper Chattahoochee and Savannah rivers is attested to by a number of species common to both drainages, besides *fraterna*.

Clench and Turner claim that *mcmichaeli* is larger than *fraterna* and that occasional specimens, "show salmon coloration [nacre]," but a comparison of the holotypes and all available series indicate that the specimens can not be distinguished morphologically.

Range. Apalachicolan region: restricted to the Choctawhatchee River system, Florida, and the upper Chattahoochee River, Georgia, of the Apalachicola River system. Southern Atlantic Slope: upper Savannah River system, South Carolina.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Elliptio (*Elliptio*) *waccamawensis* (Lea)

Plate 7: 6, 7

Unio waccamawensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Lake Waccamaw, North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 16, pl. 5, fig. 14: figured holotype USNM 84437. Lea, 1867, Obs. Unio, 11: 20. Simpson, 1914, Cat. Naiades, 2:620.

Description. Shell generally small, not reaching more than 60 mm, though occasionally reaching almost 90 mm in length. Outline elongated rhomboid. Valves inflated or subinflated, thin, inequilateral. Anterior end regularly rounded; posterior end slightly biangulate and pointed toward the base. Ventral margin quite straight. Dorsal margin rather short and straight, meeting the obliquely descending posterior margin in a usually distinct angle. Hinge ligament long and low. Posterior ridge very high, decidedly angular, with sometimes a faint second ridge above it ending behind in a broad point. Posterior slope obliquely truncate, often with wrinkled sculpture. Umbos neither high nor full, located in the anterior quarter of the shell, their sculpture not observed. Periostracum rather smooth, with delicate growth lines, generally smoky-green, sometimes yellowish or brownish, often with dark green rays over the entire surface.

Left valve with two, occasionally three, stumpy pseudocardinal teeth, one in front of the other, often of almost equal height. Hinge line very short and narrow, two rather short straight lateral teeth. Right valve with two parallel pseudocardinals, the posterior one inclined to be narrow and triangular, occasionally broken into two teeth, the more anterior tooth low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor

muscle scars and pallial line distinct. Nacre generally bluish white or pink, sometimes yellowish, somewhat iridescent.

Length mm	Height mm	Width mm	
88	45	28	A drainage canal, 1 mi. NNW Dupree Landing, Columbus Co., North Carolina.
61	34	22	As above.
54	32	22	Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co., North Carolina.

Habitat. Lives in sand, in sluggish water.

Remarks. Elliptio waccamawensis (Lea), which is restricted to the Waccamaw River system, most closely resembles *E. congaraea* (Lea) from the nearby Cape Fear River system, though *waccamawensis* is easily distinguished from it by being consistently more elongated, with a decidedly more acutely angled posterior ridge. In both species, the posterior slope has the tendency to have wrinkled sculpture, but the periostracum of *waccamawensis* tends to be more intensely green and is more inclined to be rayed.

Specimens of unionids from Lake Waccamaw have always been greatly corroded and many of their conchological characters obfuscated, but recently H. D. Athearn has taken some more perfect examples of *waccamawensis* from the obviously hospitable environment of a canal that was dug parallel to the road on the west side of the lake.

Range. Southern Atlantic Slope: restricted to the Waccamaw River system, North Carolina.

Specimens Examined

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw; Lake Waccamaw, 0.5 mi. W [town of] Lake Waccamaw; Drainage canal, beside Lake Waccamaw, 1 mi. NNW Dupree Landing; *all* Columbus Co.

Elliptio (*Elliptio*) *complanata* (Lightfoot) Plate 8: 1–6

Mya complanata (Lightfoot) 1786, Catalogue of the Portland Museum, p. 100, no. 2190 (Maryland) refers to: Lister, 1686, Synopsis Methodicae Conchyliorum, pl. 150, fig. 5 (Virginia; figured specimen Oxford Univ. Mus. [probably lost] *teste* Dance, 1966, Shell Collecting, p. 292). Type locality restricted to the Potomac River, Washington, District of Columbia [approximately opposite Fairfax Co., Virginia] by Johnson, 1948, Nautilus, 62: 36. In citing Lightfoot rather than Solander (Johnson *loc. cit.*) as the authority for this species I have followed Rehder (1967: 2, 18).

Unio violaceus Spengler 1793, Skrivter af Naturhistorie Selskabet [Copenhagen], 3: 55 (Nordamerika; holotype, Copenhagen Museum; figured by Haas, 1913, Vidensk. Meddr. Dansk Naturh. Foren. [Copenhagen], 65: 51, text fig.).

Unio purpureus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 1 (Delaware and Schuylkill Rivers [presumably near Philadelphia, Philadelphia Co., Pennsylvania], type, ANSP [lost]).

Unio rarisulcata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 72 (le lac Champlain [Vermont]; type, Cab. of M. Dufresne [lost]).

Unio coarctata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 73 (la rivière Hudson [New York]; holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 53, fig. 5).

Unio purpurascens Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 73 (les rivières de l'etat de New Yorck [*sic*]; type, Cab. of M. Valenciennes [lost]; type of var. b and c, Paris Museum, the latter selected as lectotype by Johnson, 1969, Nautilus, 83: 60, fig. 6 du lac Champlain [New York]).

Unio rhombula Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (Sénégal; [erroneous] holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 8).

Unio carinifera Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (la rivière Hudson de l'etat de New York; holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 52, fig. 4).

Unio georgina Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 74 (le lac George [New York]; holotype, Paris Museum,

figured by Johnson, 1969, Nautilus, 83: 53, fig. 3).

Unio glabrata Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 75 (la rivière de l'Ohio; [erroneous] holotype, Paris Museum, figured by Johnson, 1969, Nautilus, 83: 53, fig. 7).

Unio sulcidens Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 77 (une rivière du Connecticut; holotype, Paris Museum, Schunglkill [Schuylkill River], Pennsylvania; paratype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 3.

Unio virginiana Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6 (1): 79 (la rivière Potowmac [Potomac] en Virginie; holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coq. de Lamarck, pl. 12, fig. 4.

Unio aurata Rafinesque 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 295 (la rivière Hudson [New York]; type not in ANSP [lost]).

Unio fluviatilis Green 1827, Jour. Machurian Lyceum (Philadelphia), 1: 41. [no locality; type lost.]

Mya rigida Wood 1828, Index Testaceologicus, Supplement, pl. 1, fig. 10 (no locality; type [lost]). Wood, 1856, *op. cit.*, ed. Hanley, p. 200, pl. 1, supp. fig. 10.

Unio griffithianus Lea 1834, Trans. Amer. Philos. Soc., 5: 103, pl. 15, fig. 46 (South Carolina; figured holotype USNM 85610). Lea, 1834, Obs. Unio, 1: 215.

Unio complanatus subinflatus Conrad 1835, New Fresh Water Shells United States, Appendix, p. 5, pl. 9, fig. 2 (Savannah River [Augusta, Richmond Co., Georgia]; syntype ANSP 119985; and Congaree River, South Carolina). Conrad, 1838, Monography Unionidae, no. 11, p. 97, pl. 54, fig. 1.

Unio jejunus Lea 1838, Trans. Amer. Philos. Soc., 6: 9, pl. 4, fig. 9 (Roanoke River [road between Winton and Tarborough, North Carolina]); [Wateree River], near Camden, [Kershaw Co.], South Carolina, figured holotype USNM 85475. Lea, 1838, Obs. Unio, 2: 9.

Unio roanokensis Lea 1838, Trans. Amer. Philos. Soc., 6: 27, pl. 8, fig. 21 (Roanoke River [road between Norfolk, Virginia; and Tarborough, North Carolina] figured holotype USNM 85423; Altamaha [River], Georgia). Lea, 1838, Obs. Unio, 2: 27.

Unio fuliginosus Lea 1845, Proc. Amer. Philos. Soc., 4: 164 (Cobb's Creek, near Philadelphia [Philadelphia Co.], Pennsylvania). Lea, 1848, Trans. Amer. Philos. Soc., 10: 78, pl. 7, fig. 19; figured holotype USNM 85665. Lea, 1848, Obs. Unio, 4: 52.

Unio cuvierianus Lea 1852, Trans. Amer. Philos. Soc., 19: 263, pl. 16, fig. 16 (Washington Co., Georgia; figured holotype USNM 85401). Lea, 1852, Obs. Unio, 5: 19.

Unio errans Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Tobesaufke [Tobesofkee] Creek, near Macon [Bibb Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 60, pl. 9, fig. 42; figured holotype USNM 85541. Lea, 1858, Obs. Unio, 6: 60.

Unio vicinus Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Swift Creek, near Macon [Bibb Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 61, pl. 9, fig. 43; figured holotype USNM 85543. Lea, 1858, Obs. Unio, 6: 61.

Unio geminus Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 63, pl. 10, fig. 45; figured holotype USNM 84856. Lea, 1858, Obs. Unio, 6: 63.

Unio abbevillensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1857, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 51, pl. 6, fig. 34; figured holotype USNM 85583. Lea, 1858, Obs. Unio, 6: 51.

Unio percoarctatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 59, pl. 3, fig. 206; figured holotype USNM 85529. Lea, 1862, Obs. Unio, 8: 63.

Unio wheatleyi Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Erroneously thought preoccupied by Lea and changed to:

Unio catawbensis Lea 1861, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 54, pl. 1, fig. 200; figured holotype USNM 85547. Lea, 1861, Obs. Unio, 8: 58.

Unio insulsus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 53, pl. 1, fig. 199; figured holotype USNM 85644. Lea, 1862, Obs. Unio, 8: 57.

Unio spadiceus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Deep River, Gulf [Chatham Co.]; mountain streams; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 55, pl. 1, fig. 201; figured holotype USNM 85251, from mountain streams, North Carolina. Lea, 1862, Obs. Unio, 8: 59.

Unio macer Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 202, pl. 29, fig. 271;

figured holotype USNM 85427, labeled; Neuse River, near Raleigh [Wake Co.], North Carolina. Lea, 1863, Obs. Unio, 9: 24.

Unio contractus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 203, pl. 29, fig. 272: figured holotype USNM 86102. Lea, 1862, Obs. Unio, 9: 25.

Unio virens Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 80, pl. 16, fig. 60; figured holotype USNM 85544. Lea, 1858, Obs. Unio, 6: 80.

Unio savannahensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Savannah River, Brantley's Mill [not located], Washington Co., *both* Georgia; Santee Canal, South Carolina; Sugar Creek, Mecklenburg Co., North Carolina). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 80, pl. 16, fig. 61; figured holotype USNM 85404 from Savannah River. Lea, 1858, Obs. Unio, 6: 81.

Unio subflavus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Walnut Creek above Macon [Bibb Co.], Georgia); Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 90, pl. 19, fig. 70; figured holotype USNM 85562. Lea, 1858, Obs. Unio, 6: 90.

Unio fumatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 171 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia; Hospaliga Creek, Alabama, [and] Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 88, pl. 18, fig. 68; figured holotype USNM 85552, from Chattahoochee River. Lea, 1858, Obs. Unio, 6: 88.

Unio subniger Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [County], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 196, pl. 22, fig. 79; figured holotype USNM 85560. Lea, 1859, Obs. Unio, 7: 14.

Unio neuseensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 60, pl. 4, fig. 208; figured holotype USNM 85465. Lea, 1860, Obs. Unio, 8: 64.

Unio purus Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 61, pl. 4, fig. 209; figured holotype USNM 85003. Lea, 1860, Obs. Unio, 8: 65.

Unio exactus Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 41 (Neuse River, 6 miles from [East] Raleigh [Wake Co.], North Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 62, pl. 4, fig. 210; figured holotype USNM 85002. Lea, 1860, Obs. Unio, 8: 66.

Unio postellii Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 165 (Randall's Creek, near Columbus [Muscogee Co.]; Carter's Creek, Baldwin Co.; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 214, pl. 26, fig. 94; figured holotype USNM 85470 from Carter's Creek. Lea, 1859, Obs. Unio, 7: 32.

Unio roswellensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 165 (Chattahoochee River, Roswell, Cobb Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 205, pl. 24, fig. 87; figured holotype USNM 85467. Lea, 1859, Obs. Unio, 7: 23.

Unio burkensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 112 (Buckhead Creek, Burke Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 215, pl. 27, fig. 95; figured holotype USNM 85998. Lea, 1859, Obs. Unio, 7: 33.

Unio hallenbeckii Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Flat Rock Creek; Four Mile Creek; *both* near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 328, pl. 51, fig. 154; figured holotype USNM 85537, from Black Dirt Creek, near Columbus [Muscogee Co.], Georgia. Lea, 1860, Obs. Unio, 8: 10.

Unio baldwinensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Carter's Creek, Baldwin Co., Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 330, pl. 51, fig. 155; figured holotype USNM 85420. Lea, 1860, Obs. Unio, 8: 12.

Unio salebrosus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (Flat Rock Creek; Bull Creek; Chattahoochee River; *all* near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 332, pl. 52, fig. 157; figured holotype USNM 85574, from Flat Rock Creek. Lea, 1860, Obs. Unio, 8: 14.

Unio raeensis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Chattahoochee [River], near Columbus [Muscogee Co.] and Rae's Creek [not located], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 331, pl. 52, fig. 156; figured holotype USNM 85571. Lea, 1860, Obs. Unio, 8: 13.

Unio latus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Savannah River, near Savannah [Chatham Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 334, pl. 53, fig. 159; figured holotype USNM 85898. Lea, 1860, Obs. Unio, 8: 16.

Unio quadratus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 172 (Carter's Creek, [Baldwin Co.]; Factory Creek, near Columbus [Muscogee Co.]; *both* Georgia). Lea, 1860, Jour. Acad. Nat.

Sci. Phila., ser. 2, 4: 338, pl. 54, fig. 163; figured holotype USNM 85718 from Factory Creek. Lea, 1860, Obs. Unio, 8: 20.

Unio squameus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 391 (North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 200, pl. 28, fig. 269; figured holotype USNM 85530. Lea, 1863, Obs. Unio, 9: 22.

Unio rostrum Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 391 (Davidson Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 201, pl. 29, fig. 270; figured holotype USNM 85556. Lea, 1863, Obs. Unio, 9: 23.

Unio northamptonensis Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 392 (Connecticut River, Northampton [Hampshire Co.]; [Connecticut River] Springfield [Hampden Co.]; *both* Massachusetts. [Connecticut River] below Hartford [Hartford Co.], Connecticut; Neuse River, North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 190, pl. 25, fig. 260; figured holotype USNM 85527 from the Connecticut River, Northampton [Hampshire Co.], Massachusetts. Lea, 1863, Obs. Unio, 9: 12.

Unio decumbens Lea 1861, Proc. Acad. Nat. Sci. Phila., 14: 40 (Alabama). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 87, pl. 12, fig. 236; figured holotype USNM 86150 [not seen]. Lea, 1862, Obs. Unio, 8: 91. Is *E. complanata, fide* Frierson, 1922, Nautilus, 36: 44.

Unio raleighensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Neuse River, 6 mi. East of Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 6, pl. 1, fig. 2; figured holotype USNM 85592. Lea, 1867, Obs. Unio, 11: 10.

Unio aberrans Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Neuse River, 6 mi. East of Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 7, pl. 1, fig. 3, figured holotype USNM 85600. Lea, 1867, Obs. Unio, 11: 1.

Unio weldonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 11, pl. 3, fig. 8; figured holotype USNM 85407. Lea, 1867, Obs. Unio, 11: 15.

Unio mecklenbergensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (near Charlotte, Mecklenberg [*sic*] Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 17, pl. 5, fig. 15, figured holotype USNM 85419. Lea, 1867, Obs. Unio, 11: 21.

Unio chathamensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Rocky Run, Chatham Co., North Carolina; James River, near Richmond [Henrico Co.], Virginia). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 21, pl. 6, fig. 19; figured holotype USNM 85672 from Rocky Run. Lea, 1867, Obs. Unio, 11: 25.

Unio gastonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 (Mine Creek, Gaston Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 20, pl. 6, fig. 18; figured holotype USNM 85409. Lea, 1867, Obs. Unio, 11: 24.

Unio quadrilaterus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Abbeville District [Savannah River drainage], South Carolina; Neuse River, near [6 miles East of] Raleigh [Wake Co.]; Catawba River; *both* North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 5, pl. 1, fig. 1; figured holotype USNM 85385 from the Neuse River. Lea, 1867, Obs. Unio, 11: 9.

Unio indefinitus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Long Creek, Mecklenburg Co.; Neuse River, near [6 miles East of] Raleigh [Wake Co.]; *both* North Carolina). Changed to:

Unio indefinitus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 15, pl. 4, fig. 12; figured holotype USNM 85388, from Long Creek. Lea, 1867, Obs. Unio, 11: 19.

Unio cistelliformis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, near [6 miles East of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 19, pl. 6, fig. 17; figured holotype USNM 85533. Lea, 1867, Obs. Unio, 11: 23.

Unio mediocris Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, [6 miles East of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 24, pl. 7, fig. 22; figured holotype USNM 85611. Lea, 1866, Obs. Unio, 11: 28.

Unio perlucens Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Six Runs, Sampson Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 18, pl. 5, fig. 16; figured holotype USNM 85076. Lea, 1867, Obs. Unio, 11: 22.

Unio curatus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Sugar Creek [Mecklenburg Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 23, pl. 7, fig. 21; type, C. M. Wheatley collection in ANSP; the only specimen located, ANSP 127200, is not figured type. Lea, 1867, Obs. Unio, 11: 27.

Unio protensus Lea 1865, Proc. Acad. Nat. Sci. Phila., 17: 33 (North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 256, pl. 31, fig. 71; figured holotype USNM 85994, from Eno River, near Hillsboro, Orange Co., North Carolina. Lea, 1868, Obs. Unio, 12: 16.

Unio lazarus Sowerby 1868 *in* Reeve, Conch. Iconica 16, *Unio,* pl. 68, fig. 348 (Abbeville

District [Savannah River drainage], South Carolina) *non* Lea, 1852.

Unio beaverensis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Beaver Creek [Gaston Co.]; Long Creek [Gaston Co.]; *both* North Carolina. Carter's Creek [Baldwin Co.], Georgia). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 297, pl. 44, fig. 109; figured holotype USNM 85598 from Beaver Creek. Lea, 1869, Obs. Unio, 12: 57.

Unio nubilus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek, Mecklenburg Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 298, pl. 44, fig. 110; figured holotype USNM 85417. Lea, 1869, Obs. Unio, 12: 58.

Unio datus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek [Mecklenburg Co.]; Beaver Co. [= Creek, Gaston Co.]; Long Creek [Gaston Co.]; *all* North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 299, pl. 44, fig. 111; figured holotype USNM 85097 labeled, "Paw Creek, Beaver Co., North Carolina." Lea, 1869, Obs. Unio, 12: 59.

Unio humerosus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Charlotte, Mecklenburg Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 301, pl. 45, fig. 113; figured holotype USNM 85414. Lea, 1869, Obs. Unio, 12: 61.

Unio uharecnsis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 145 (Uharee [Uwharree] River, Montgomery Co., North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 304, pl. 46, fig. 116; figured holotype USNM 85576. Lea, 1869, Obs. Unio, 12: 63.

Unio tortuosus Sowerby 1868, Conch. Iconica, 16, *Unio,* pl. 65, fig. 330 (Maryland; figured holotype BMNH 74.12.11.25).

Unio santeensis Lea 1871, Proc. Acad. Nat. Sci. Phila., 23: 193 (Santee Canal, South Carolina; Oconee River, Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 20, pl. 6, fig. 17; figured holotype USNM 85635, from Santee Canal. Lea, 1874, Obs. Unio, 13: 24.

Unio yadkinensis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 156 (Yadkin River, near Salisbury [Rowan Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 32, pl. 10, fig. 29; figured holotype USNM 85387. Lea, 1874, Obs. Unio, 13: 36.

Unio amplus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 39, pl. 13, fig. 36; figured holotype USNM 85591. Lea, 1874, Obs. Unio, 13: 43.

Unio ligatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Irwin's Creek, Mecklenburg Co.; Long Creek, Gaston Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 49, pl. 17, fig. 47; figured holotype USNM 85590, from Irwin's Creek. Lea, 1874, Obs. Unio, 13: 53.

Unio differtus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 ([Savannah River], Georgia ?). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 42, pl. 14, fig. 39; figured holotype USNM 85399. Lea, 1874, Obs. Unio, 13: 46.

Unio subparallelus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Irwin's Creek [Mecklenburg Co.]; Fox River [not located]; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 46, pl. 16, fig. 44; figured holotype USNM 85418, localities not separated. Lea, 1874, Obs. Unio, 13: 50.

Unio oblongus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 158 (Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 52, pl. 18, fig. 50; figured holotype USNM 85572. Lea, 1874, Obs. Unio, 13: 56.

Unio curvatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Pfeiffers Pond [Charlotte], Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 47, pl. 13, fig. 35; figured holotype USNM 85550. Lea, 1874, Obs. Unio, 13: 42.

Unio irwinensis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Irwin's Creek, [Mecklenburg Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 44, pl. 15, fig. 42; figured holotype USNM 85680. Lea, 1874, Obs. Unio, 13: 48.

Unio subsquamosus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Yadkin River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 47, pl. 16, fig. 45; figured holotype USNM 85557. Lea, 1874, Obs. Unio, 13: 51.

Unio infuscus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Fox River [not located]; Irwin's Creek, Mecklenburg Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 51, pl. 17, fig. 49; figured holotype USNM 85587 from Fox River. Lea, 1874, Obs. Unio, 13: 55.

Unio ratus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Neuse River, North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 52, pl. 18, fig. 51; figured holotype USNM 85382. Lea, 1874, Obs. Unio, 13: 56.

Unio basalis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 161 (Carter's Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 48, pl. 16, fig. 46; figured holotype USNM 85703. Lea, 1874, Obs. Unio, 13: 52.

Unio dissimilis Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 161 (Long Creek, Gaston Co.; Pfeiffers Pond, [Charlotte], Mecklenburg Co.; *both* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 53, pl. 18, fig. 52; figured holotype USNM 86019 from Long Creek. Lea, 1874, Obs. Unio, 13: 57.

Unio cirratus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 55, pl. 19, fig. 53; figured holotype USNM 85584. Lea, 1874, Obs. Unio, 13: 59.

Unio subolivaceus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Catawba River; Fox River [not located]; Yadkin River; *all* North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 57, pl. 20, fig. 56; figured holotype USNM 85564. Lea, 1874, Obs. Unio, 13: 61.

Unio infulgens Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 422 (Stewart's Pond, Union Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 60, pl. 21, fig. 59; figured holotype USNM 85403. Lea, 1874, Obs. Unio, 13: 64.

Unio corneus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 423 ([Chattahoochee River] Columbus [Muscogee Co.]; Marietta [Cobb Co.]; *both* Georgia. Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 59, pl. 20, fig. 58; figured holotype USNM 85580. Lea, 1874, Obs. Unio, 13: 63.

Unio dooleyensis Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 (Flint River, Dooley Co., Georgia; Abbeville District [Savannah River drainage] South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 64, pl. 22, fig. 60; figured holotype USNM 85538 from Flint River. Lea, 1874, Obs. Unio, 13: 68.

Unio gesnerii Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 (Uchee River [Russell Co., Alabama], near Columbus [Muscogee Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 65, pl. 22, fig. 64; figured holotype USNM 85670. Lea, 1874, Obs. Unio, 13: 69.

Unio invenustus Lea 1874, Proc. Acad. Nat. Sci. Phila. for 1873, 25: 424 ([Chattahoochee River] Columbus [Muscogee Co.]; Russell Co.; *both* Georgia. Irwin's Creek [Mecklenburg Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 66, pl. 22, fig. 62; figured holotype USNM 85704 from Columbus, Georgia. Lea, 1874, Obs. Unio, 13: 70.

Unio (*Arconaia*) *provancheriana* Pilsbry 1890, Nat. Canadienne, 20: 171 (locality unknown). Pilsbry, 1891, Nautilus, 4: 127. Pilsbry, 1892, Proc. Acad. Nat. Sci. Phila., 44: 132, pl. 7, figs. 4–6; figured holotype ANSP 63094.

Unio palliatus 'Ravenel' Simpson 1900, Proc. United States Natl. Mus., 22: 730. [*nomen nudum*]. Listed under the synonymy of *Unio errans* Lea.

Unio pullatus majusculus De Gregorio 1914, Il Naturalista Siciliano, 22: 57, pl. 8, figs. a–d (Connecticut; type Palermo Museum, Sicily [not seen]).

Unio complanatus mainensis Rich 1915, Science, n. s., 42: 580 (Songo Pond about 3 miles South of Bethel [Oxford Co.], Maine; type, [location not known]).

Elliptio violaceus (Spengler). Ortmann, 1919, Mem. Carnegie Mus., 8: 94, pl. 8, figs. 4, 5.

Elliptio strigosus (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Elliptio complanatus (Solander). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 21, figs. 26–28. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull., 183, p. 22, pl. 1, figs. 5, 6; pl. 4, figs. 7, 8.

Description. Shell large, often reaching over 100 mm in length. Outline generally long, trapezoidal, sometimes decidedly rhomboid, occasionally subelliptical. Valves generally flat or subinflated, though occasionally considerably inflated, thin to solid. Anterior end regularly rounded; posterior end usually broader and somewhat biangulate. Ventral margin straight or slightly arcuate, roughly parallel to the long straight or slightly curved dorsal margin, which forms an obtuse angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge usually broad, double and rounded, sometimes rather angular, ending in a biangulation near the base. Posterior slope broad and unsculptured. Umbos low and uninflated, their sculpture consisting of strong ridges that run nearly parallel to the growth lines and are carried back to the nucleus behind as delicate radial lirae. Surface with irregular growth lines, often nearly smooth in young shells, becoming rougher in old ones. Periostracum brownish, or yellowish green, greenish brown, to almost black, often with green rays over the entire surface.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, the more anterior one triangular, the hinder one generally not much elevated above the hinge line. Hinge line short and narrow; two long, straight, granular lateral teeth. Right valve with one chunky, serrated pseudocardinal, with a vestigial tooth in front of it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally purplish, though often white, or slightly orange; iridescent, especially toward the margins.

Length mm	Height mm	Width mm	
154	82	44	Tar River, Bruce, 9 mi. NW Greenville, Pitt Co., North Carolina.
99	50	28	Savannah River, 7 mi. NE Newington, Screven Co., Georgia.
77	43	20	Turkey Creek, 4 mi. NE Allentown, Wilkinson Co., Georgia.

Anatomy. See Ortmann (1912a: 269). Discussed and figured by Reardon (1929: 11, pl. 4, figs. 1–10).

Breeding season. Ortmann (1919: 104) found gravid females from April 26 through July 16 during several years in Pennsylvania; the breeding season was restudied by Matteson (1948b: 704), who found that in the Ocqueoc River, lower Michigan, it extended from the middle of June to the middle of July.

Habitat. Found in lakes, ponds, small streams, and large rivers on nearly every type of substrate, though it appears to prefer sand. Throughout its range it is sometimes the only unionid found at some stations, and at others it is generally found in greater numbers than any other species save where its distribution overlaps *Elliptio icterina* (Conrad).

Remarks. Elliptio complanata (Lightfoot), which is found at scattered localities in the Apalachicola River system, is the most widely distributed and abundant unionid in the Atlantic Slope region, extending from the upper Altamaha River, Georgia, to northern Canada. It is a very variable species, but most nineteenth century authors agreed on uniting all of the ecophenotypes north of about the latitude of Washington under *complanata.* South of Washington, Isaac Lea, especially when in his seventies and eighties, applied specific names to the ecophenotypes of *complanata* and *icterina* as assiduously as Bourguignat and Locard did to the common European unionids, with the same confusion resulting. Simpson (1914, 2: 651) did a great deal to rectify the synonymy of *complanata.* This species, although variable in outline, degree of inflation, and color of both periostracum and nacre, is generally trapezoidal in outline, with the valves rather compressed, and when swollen, the greatest width is in the region of the posterior ridge. In large rivers such as the Savannah, Neuse, Tar, Roanoke, lower Potomac, and Connecticut, specimens reach maximum size, and tend to be subelliptical in outline with flattened valves, whereas in smaller rivers and tributaries they tend to be more rhomboid in outline and more inflated. Walter (1956: 266, 270) regarded the small creek form as *E. c. complanata* and called the large river form *E. complanata roanokensis* (Lea), even though both forms were found together at a number of the stations.

In the Altamaha River system *E. complanata* can be confused with *E. hopetonensis* (Lea) (under which see: *Remarks* on p. 325) which replaces it in the Altamaha River proper. It can also be confused with *E. icterina* (Conrad) (under which see: *Remarks* on p. 328) with whose several ecophenotypes it is often found, south of the White Oak River, North Carolina. In Georgia, *complanata* can not be confused with *Uniomerus tetralasmus* (Lea) with its acutely angled meeting of

the dorsal and posterior margins and its satiny periostracum. These characteristics become somewhat less constant in the Carolinas and northward, and *complanata* can be confused with it. However, *tetralasmus* tends to be more quadrate and to exhibit more swelling of the valves, and is always unrayed.

The specimens of *E. complanata* from Lake Creek, at Stone Mountain, De Kalb Co., Georgia, are among just a few records of Unionidae collected above the Fall Line in Georgia. Unfortunately, I misidentified them as *hopetonensis* for Raulerson and Burbank (1962, 9: 39).

Range. Apalachicolan region: restricted to the Apalachicola River system. Atlantic Slope region: Altamaha River system, Georgia, north to the St. Lawrence River system, Canada. Interior Basin: westward to Lake Superior, also parts of the Hudson Bay drainage. Discussed in detail and illustrated by Matteson (1948a: 13, fig. 2).

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Lake Creek at Stone Mountain, De Kalb Co. Walnut Creek, E Macon; Tobesofkee Creek, 5 mi. S Macon (USNM); *both* Bibb Co. Flat Creek, 2 mi. S Perry; Big Creek, 3 mi. S Henderson; *both* Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Cedar Creek, 5 mi. WSW Hawkinsville; Tuscawhatchee Creek, 5 mi. SW Hawkinsville; *all* Pulaski Co. Bluff Creek, 8 mi. NW Abbeville, Wilcox Co. Dicksons Creek, 10 mi. NW Fitzgerald, Ben Hill Co.

Oconee River Drainage. *Georgia*: Carters Creek, Baldwin Co. Turkey Creek, 4 mi. NE Allentown, Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville, Johnson Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee Creek, 4 mi. SW Mitchell, Glascock Co. Big Creek, 3 mi. SE Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; Big Creek, 3 mi. E Louisville; *all* Jefferson Co. Mill Creek, 5 mi. E Midville; Buckhead Creek, 14 mi. W Waynesboro; Buckhead Creek, 10 mi. SW Waynesboro; *all* Burke Co. Ogeechee River, Scarboro (MZUM); Ogeechee River, bridge, 1 mi. S Dover (MZUM); *both* Screven Co. Ogeechee River, bridge, 1 mi. E Blitchton (MZUM); Ogeechee River, Jinks Bridge, Route 16 (MZUM); Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke (MZUM); *all* Bryan Co.

Savannah River System

Broad River Drainage. *Georgia*: Cadya Creek [not located] (MZUM). Broad River, 1.5 mi. S Bell; Broad River, Huguenot; *both* Elbert Co.

Savannah River Drainage. *South Carolina:* Abbeville Co. (USNM). Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia:* Savannah River, Augusta, Richmond Co. (MZUM). *South Carolina:* Lower Three Runs Creek, 8 mi. SW Barnwell, Barnwell Co.; Savannah River, 6 mi. W. Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, King Jaw Point, 10 mi. WSW Allendale (MZUM); *all* Allendale Co. *Georgia:* Brier Creek, Keysville (MZUM); Mill Race, 2 mi. N Sardis; *both* Burke Co. Savannah River, 7 mi. NE Newington, Screven Co. *South Carolina:* Mouth of Vermezobre Creek (Savannah River Wildlife Res.), Jasper Co. (MZUM). Savannah River, Savannah, Chatham Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Lemon Creek, 2.5 mi. S Bam-

berg; Little Salkehatchee River, 4 mi. N Ehrhardt; *both* Bamberg Co. Whippy Swamp Creek, 2.5 mi. NE Crocketville, Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Snake Swamp Creek, Orangeburg Co., 6 mi. NE Bamberg, Bamberg Co. N. Fork Edisto River, Orangeburg, Orangeburg Co. Edisto River, Givhans Ferry, 2 mi. NW Givhans, Dorchester Co.

Ashley River System

Ashley River Drainage. *South Carolina*: [Ashley River] near Summersville, Dorchester Co.

Cooper-Santee River System

Saluda River Drainage. *South Carolina:* Saluda River, 2.3 mi. above Ware Shoals, Abbeville Co.

Broad River Drainage. *Tennessee*: Green River, 5 mi. ENE Mill Spring, Polk Co. *South Carolina:* Headwaters, Broad River, SE Reidsville, Spartenburg Co.

Congaree River Drainage. *South Carolina:* Congaree River, Columbia, Richland Co.

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. Leppers Creek, Lincolnton, Lincoln Co. Mine Creek; Beaver Creek; *both* Gaston Co. Paw Creek; Stewarts Creek; Irwins Creek; Sugar Creek; Ashleys Creek; Long Creek; Catawba River; Bissels Pond, Charlotte; Pfeiffers Pond, Charlotte; Elias Pond, 10 mi. from Charlotte; *all* Mecklenburg Co. *South Carolina:* Branch, Little Dutchmans Creek, Rockhill, York Co.

Wateree River Drainage. *South Carolina*: Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co., Wilsons Landing, 5 mi. NW Pineville; Santee Canal; *both* Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Sammy Swamp Creek, 6 mi. S Paxville, Clarendon Co.

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Yadkin River Drainage. *North Carolina:* Yadkin River, Boomville, Yadkin Co. Yadkin River, Salisbury, Rowan Co. (MZUM). Ditch, Buffalo Creek, 6 mi. E Concord, Cabarrus Co. (MZUM). Uwharrie River, Montgomery Co. (USNM). Stewarts Pond, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co. *South Carolina:* Ditch, Waccamaw River, 1.25 mi. SE Conway, Horry Co. Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Sandy Creek, Randolph Co. (MZUM). Rocky Run (USNM); Deep River, Gulf (Lea); *both* Chatham Co.

Cape Fear River Drainage. *North Carolina:* Haw River, 1.25 mi. NE Benaja, Rockingham Co. (MZUM). Buffalo Creek, 1 mi. E Greensboro, Guilford Co. (MZUM). Morgan Creek, 1 mi. SE Chapel Hill, Orange Co. (MZUM). New Hope River, Burke Forest, Durham Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. Cape Fear River, Carlos; Cape Fear River, Kinnon; *both* Cumberland Co. (*both* MZUM). Ashe River, Pender Co. Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

South River Drainage. *North Carolina*: Six Runs, Sampson Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro Center,

Person Co. (81)[1] Eno River, 1.75 mi. ESE Hillsboro Center (117); S Fork, Little River, 0.5 mi. N Schley (104); Lake Michie, 12 mi. NNE Durham Center (75); Neuse River, 6 mi. ENE Durham Center (64); *all* Durham Co. Neuse River, 10.5 mi. NE Raleigh (49); Walnut Creek, 4.75 mi. WSW Raleigh (32); Swift Creek, 3 mi. WSW Garner (21); *all* Wake Co. Little River, 1.25 mi. NW Bagley (2); Neuse River, 3.5 mi. NNE Smithfield (26); *both* Johnston Co. Neuse River, Cliffs of Neuse State Park, 2 mi. NW Seven Springs, Wayne Co. Neuse River, 13.5 mi. WSW Kingston Center, Lenoir Co. Neuse River, Streets Ferry, 8.5 mi. NNW New Bern, Craven Co. Trent River, near Pollocksville, Jones Co. (MZUM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. Sandy Creek, Franklin Co. Stony Creek, Nashville, Nash Co. [Beach Swamp Creek] Enfield, Halifax Co. Swift Creek, Whitakers (MZUM); Tar River, Tarboro; Tar River, Old Sparta, 3.5 mi. W Pinetops; *all* Edgecomb Co. Tar River, Bruce, 9 mi. NW Greenville; Mill Run, Greenville; *both* Pitt Co.

Roanoke River System

Dan River Drainage. *Virginia*: Aarons Creek, 3 mi. W Buffalo Lithia Springs; Dan River; *both* Halifax Co. Bluestone Creek, near Clarksville, Mecklenburg Co.

Roanoke River Drainage. *Virginia*: Roanoke River, 4 mi. SW Elliston; N. Fork Roanoke River, Ironto (USNM); *both* Montgomery Co. Black Water River, Franklin Co. (MZUM). *North Carolina:* Roanoke River, Washington Co.

Chowan River System

Meherrin River Drainage. *Virginia*: Meherrin River, 2 mi. SW Grandy, Brunswick Co. Three Creek, near Emporia, Greensville Co. (MZUM). *North Carolina*: Meherrin River, Murfreesboro, Hertford Co. (USNM).

Nottoway River Drainage. *Virginia*: Tommeheton Lake, near Camp Pickett, Nottoway Co. Waqua Creek, 2 mi. SE Rawlings; Nottoway River, 3 mi. E Rawlings; *both* Brunswick Co.

Blackwater River Drainage. *Virginia*: Swift Creek, Rolling Mills, Chesterfield Co. Nansemond River, Nansemond Co.

Chowan River Drainage. *Virginia*: Chowan River, Edenhouse, 13 mi. E Windsor, Bertie Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407). North [= Maury] River, Lexington, Rockbridge Co. (USNM). Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. James River, near Cartersville, Cumberland Co. James River, Richmond, Henrico Co. (MZUM).

Chickahominy River Drainage. *Virginia:* Chickahominy River, 4 mi. S Ashland, Hanover Co.

York River System

North Anna River Drainage. *Virginia*: Mine Run; Church River; *both* Orange Co., (*both* MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Mountain Run, Orange Co. (USNM).

Rappahannock River Drainage. *Virginia:* Rappahannock River, 1 mi. S Remington, Faquier Co. Mountain Run, 3 mi. N

[1] Walter (1956) marked on a map of the Upper Neuse River some of the 136 stations he made during his survey in 1950–51. He collected *E. complanata* at forty of them. A selection of these with the station numbers included are presented here, since the localities have never been published. According to the author, most of the collections were made with a 1/8 inch mesh scraper net, which accounts for the paucity of specimens in most of the lots and also why this and other species were not found at more of the stations.

Lignum, Culpeper Co. Rappahannock River, Fredericksburg, Spotsylvania Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Bull Run, 3 mi. N Catharpin; Broad Run, [Fairfax Co.], 3 mi. W Manassas; Kettle Run, 1.5 mi. N Nokesville; *all* Prince William Co.

Potomac River System

Potomac River Drainage. *West Virginia:* Cacapon River, 1 mi. below Intermont, Hampshire Co. (USNM). Potomac River, Brosius, Morgan Co. Canal at Harpers Ferry, Jefferson Co. (MZUM). *Virginia:* [North River of S Fork Shenandoah River], Weyers Cave, Augusta Co. Passage Creek, 2 mi. SW Seven Fountains (USNM); N Fork Shenandoah River, E Woodstock; *both* Shenandoah Co. *Maryland*: Potomac River, 0.75 mi. W Point of Rocks, Frederick Co. *Virginia:* Potomac River, near Great Falls; Little Hunting Creek, near Mt. Vernon (MZUM); *both* Fairfax Co.

Elliptio (*Elliptio*) *hopetonensis* (Lea)

Plate 9: 1–2

Unio hopetonensis Lea 1838, Trans. Amer. Philos. Soc., 6: 29, pl. 9, fig. 24 ([Altamaha River] Hopeton, near Darien [McIntosh Co.], Georgia; figured holotype USNM 85391). Lea, 1838, Obs. Unio, 2: 29. Simpson, 1914, Cat. Naiades, 2: 668.

Unio inusitatis Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Swift Creek, below Macon [Bibb Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 333, pl. 52, fig. 158; figured holotype USNM 85531. Lea, 1860, Obs. Unio, 8: 15. Simpson, 1914, Cat. Naiades, 2: 670.

Description. Shell large, often exceeding 150 mm in length. Outline subrhomboid, narrower anteriorly. Valves rather flat to subinflated, occasionally quite inflated, the greatest inflation being about midway along the posterior ridge, they are thin to solid, inequilateral. Anterior end regularly rounded; posterior end broader, wedge-shaped or slightly biangulate. Ventral margin generally straight or slightly arcuate. Dorsal margin long and straight, tending to be a bit winglike where it joins the obliquely descending posterior margin in either a sharp or imperceptible angle. Hinge ligament prominent. Posterior ridge usually rather broad, single, and narrowly rounded above, becoming double below and ending in a wide biangulation at or above the posterior base. Posterior slope rather broad and unsculptured. Umbos low, slightly inflated, located in the anterior third of the shell, their sculpture consisting of several bars. Disk rather flat, or slightly concave when a slight umbonal-ventral sulcus is present. Periostracum brownish or yellowish green to olive green, often with green rays in young individuals, becoming rough and brownish or blackish in matures.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, the more anterior one triangular, the hinder one generally not much elevated above the hinge line. Hinge line short and narrow, two long, straight, granular lateral teeth. Right valve with one chunky, serrated pseudocardinal, with a vestigial tooth in front of it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally white or pinkish, occasionally purplish and iridescent, especially toward the margins.

Length mm	Height mm	Width mm	
150	75	38	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
103	55	37	Ohoopee River, 3 mi. N Leman, Emanuel Co., Georgia.
84	43	20	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 415).

Habitat. Lives in sand or sandy mud in

the Altamaha River and its major tributaries.

Remarks. *Elliptio hopetonensis* (Lea), which is restricted to the Altamaha River system, is sympatric with *Elliptio complanata* (Lightfoot), which replaces *hopetonensis* in the smaller streams of the system. While *E. complanata* is very variable in both outline and degree of inflation, *E. hopetonensis* is quite constant in outline and in its lack of inflation. When somewhat inflated, as it is at the limits of its range, the greatest degree is near the mid portion of the posterior ridge. The posterior ridge is better defined in *hopetonensis* and the long dorsal margin tends to render most individuals wedge-shaped.

The large river form of *E. complanata* is admittedly very close to *hopetonensis*, but in river systems other than the Altamaha, where the large flat-sided form is found, more typical intergrades are generally present.

E. hopetonensis (Lea) has been confused with older specimens of *E. dariensis* (Lea), but the latter has a proportionally higher shell, with a sharper posterior ridge, often with sculpture on the posterior slope.

Range. Southern Atlantic Slope: restricted to the lower Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek below Macon, Bibb Co. Ocmulgee River, Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. House Creek, Bowens Mill, 10 mi. N Fitzgerald, Ben Hill Co. Ocmulgee River, 1.5 mi. S Jacksonville, Telfair Co.

Little Ocmulgee River Drainage. *Georgia:* Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 8 mi. SW Soperton, Treutlen Co. Oconee River, 2.5 mi. N Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, Norristown; Ohoopee River, 3 mi. N Leman; *both* Emanuel Co. Ohoopee River, above Reidsville, Tattnall Co. (ANSP).

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Jeff Davis Co. Altamaha River, 10 mi. N Baxley, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NE Everett City, Glynn Co. Altamaha River, near Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Elliptio (*Elliptio*) *icterina* (Conrad)

Plate 9: 3–10
Plate 10: 1–3

Unio icterinus Conrad, [May] 1834, New Fresh Water Shells United States, p. 41, pl. 6, fig. 5 (muddy shore, Savannah River, opposite Augusta [Richmond Co.], Georgia; figured holotype ANSP 41381). Published in May, *teste* Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 244, and not disputed by Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 336–349. Conrad, 1836, Monography Unionidae, no. 4, p. 39, pl. 18, fig. 2.

Unio raveneli Conrad, [May] 1834, New Fresh Water Shells United States, p. 39, pl. 6, fig. 4 (Wateree Canal; since found in the small creeks near Cooper River; vicinity of Santee Canal; *all* South Carolina. Two syntypes ANSP 41370; the smaller one agrees with Conrad's description, but is not the figured specimen, which appears to be *Elliptio complanata* (Lightfoot). The second specimen is *Elliptio lanceolata* (Lea), *non Unio ravenelianus* Lea, 1834).

Unio watereensis Lea 1836, Synopsis Unionidae, p. 31. New name for *Unio raveneli* Conrad, 1834, *non Unio ravenelianus* Lea, 1834. As pointed out by Simpson, 1900, Proc. United States Natl. Mus., 22: 748, this change was unnecessary.

Unio confertus Lea, [August or September] 1834, Trans. Amer. Philos. Soc., 5: 103, pl. 16, fig. 47 (Santee Canal, South Carolina; type not in USNM [presumed lost]). Lea, 1834, Obs. Unio, 1: 215. Published in August or September 1834, *teste* Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 244.

Unio lugubris Lea 1834, Trans. Amer. Philos.

Soc., 6: 30, pl. 9, fig. 25 ([Altamaha River], Hopeton, near Darien [McIntosh Co.], Georgia; figured holotype USNM 85638). Lea, 1838, Obs. Unio, 2: 30, *non* Say, 1832.

Unio geddingsianus Lea 1840, Proc. Amer. Philos. Soc., 1: 285 (Congaree River, South Carolina). Lea, 1842, Trans. Amer. Philos. Soc., 8: 202, pl. 11, fig. 15; figured holotype USNM 85650. Lea, 1842, Obs. Unio, 3: 40.

Unio fuscatus Lea 1843, Desc. Twelve Uniones (Black Creek, Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 277, pl. 40, fig. 4; figured holotype USNM 85243. Lea, 1848, Obs. Unio, 4: 35.

Unio occultus Lea 1843, Desc. Twelve Uniones (Black Creek; Lake Monroe; *both* Florida). Lea, 1846, Trans. Amer. Philos. Soc., 9: 279, pl. 41, fig. 7; figured holotype USNM 85247, from Black Creek. Lea, 1848, Obs. Unio, 4: 37.

Unio limatulus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 154 (Savannah River, [Georgia]; type not in ANSP, [presumed lost]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 276, pl. 37, fig. 9. Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 251.

Unio tuomeyi Lea 1852, Trans. Amer. Philos. Soc., 10: 256, pl. 13, fig. 4 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85669). Lea, 1852, Obs. Unio, 5: 12.

Unio whitcianus Lea 1852, Trans. Amer. Philos. Soc., 10: 258, pl. 14, fig. 8 (near Savannah [Chatham Co.], Georgia; figured holotype USNM 85658). Lea, 1852, Obs. Unio, 5: 14.

Unio barrattii Lea 1852, Trans. Amer. Philos. Soc., 10: 256, pl. 13, fig. 5 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 86010). Lea, 1852, Obs. Unio, 5: 12.

Unio pullatis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (creeks near Columbus [Muscogee Co.], Georgia). Changed to:

Unio pullatus Lea 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4:57, pl. 8, fig. 39; figured holotype USNM 86020. Lea, 1858, Obs. Unio, 6: 57.

Unio coruscus Gould 1856, Proc. Boston Soc. Nat. Hist., 6: 15 (River Saint John's, near Lake Beresford, Florida; measured holotype MCZ 169097, figured by Frierson, 1911, Nautilus, 25, pl. 1, figs. 1–3, and by Johnson, 1964, United States Natl. Mus., Bull. no. 239, p. 60, pl. 32, fig. 3).

Unio micans Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co.; Deep River, Gulf [Chatham Co.]; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 59, pl. 3, fig. 207; figured holotype USNM 85077 from the Catawba River. Lea, 1862, Obs. Unio, 8: 63.

Unio obnubilus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 84, pl. 17, fig. 64; figured holotype USNM 85646. Lea, 1858, Obs. Unio, 6: 84.

Unio opacus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 86, pl. 18, fig. 66; figured holotype USNM 85546. Lea, 1858, Obs. Unio, 6: 86.

Unio similis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 91, pl. 19, fig. 71; figured holotype USNM 85653. Lea, 1858, Obs. Unio, 6: 91.

Unio sublatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 169 ([Chattahoochee River], Uchee Bar, below Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 82, pl. 16, fig. 62; figured holotype USNM 85897. Lea, 1858, Obs. Unio, 6: 82.

Unio viridicatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 87, pl. 18, fig. 67; figured holotype USNM 85551. Lea, 1858, Obs. Unio, 6: 87.

Unio tetricus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Flint River, near Albany [Dougherty Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 195, pl. 22, fig. 78; figured holotype USNM 85655. Lea, 1859, Obs. Unio, 7: 13.

Unio aequatus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co., Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 89, pl. 19, fig. 69; figured holotype USNM 85561. Lea, 1858, Obs. Unio, 6: 89.

Unio aquilus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, Macon [County], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 92, pl. 20, fig. 72; figured holotype USNM 85993. Lea, 1858, Obs. Unio, 6: 92.

Unio viridiradiatus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 154 (Big Uchee River [Creek, Russell Co., Alabama] near Columbus, Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 336, pl. 53, fig. 161; figured holotype USNM 86018). Lea, 1860, Obs. Unio, 8: 18.

Unio hepaticus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 154 (Salkehatchie River, South Carolina). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 348, pl. 57, fig. 173; figured holotype USNM 85559. Lea, 1860, Obs. Unio, 8: 30.

Unio viridans Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 170 (near Columbus [Muskogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 337, pl. 54, fig. 162; figured holotype USNM 85579. Lea, 1860, Obs. Unio, 8: 19.

Unio verutus Lea 1859, Proc. Acad. Nat. Sci. Phila., 11: 171 (Flat Rock Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 335, pl. 53, fig. 160; figured holotype USNM 85899. Lea, 1860, Obs. Unio, 8: 17.

Unio ocmulgéensis Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 38 (Little Ocmulgee River, Lumber City [Telfair Co.], Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 95, pl. 14, fig. 243; figured holotype USNM 85901. Lea, 1862, Obs. Unio, 8: 99.

Unio merceri Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Lee Co., [Flint River drainage], Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 209, pl. 31, fig. 278, figured holotype USNM 86057. Lea, 1863, Obs. Unio, 9: 31.

Unio lucidus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co., [NE corner of Columbus Co., Cape Fear River drainage], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 9, pl. 2, fig. 6; figured holotype USNM 85242. Lea, 1867, Obs. Unio, 11: 13.

Unio livingstonensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co., [NE corner of Columbus Co., Cape Fear River drainage] North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila, ser. 2, 6: 14, pl. 4, fig. 11; figured holotype USNM 85536. Lea, 1867, Obs. Unio, 11: 18.

Unio ablatus [*sic*] Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Long Creek, Gaston Co., North Carolina). Changed to:

Unio oblatus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 13, pl. 4, fig. 10; figured holotype USNM 86001. Lea, 1867, Obs. Unio, 11: 17.

Unio radiolus Lea 1871, Proc. Acad. Nat. Sci. Phila., 23: 192 (Ogeechee River, Liberty Co., Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 21, pl. 6, fig. 18; figured holotype USNM 85621. Lea, 1874, Obs. Unio, 13: 25.

Unio cuspitatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Buckhead Creek, Burke Co., Georgia; Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 43, pl. 14, fig. 50; figured holotype USNM 86014, from Buckhead Creek. Lea, 1874, Obs. Unio, 13: 47.

Unio hastatus Lea 1873, Proc. Acad. Nat. Sci. Phila., 25: 423 (New Market, Abbeville District [Savannah River drainage], South Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 56, pl. 19, fig. 54; figured holotype USNM 86013. Lea, 1874, Obs. Unio, 13: 60.

Unio fryanus B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 113, pl. 2, fig. 1 (Lake Ashby, Volusia Co., Florida; figured holotype USNM 151032, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 5).

Unio nolani B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 116, pl. 4, fig. 11 (a creek flowing into St. Johns River, near Palatka [Putnam Co.], Florida; holotype USNM 151030, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 7, pl. 10, fig. 4).

Unio simpsoni B. H. Wright 1888, Proc. Acad. Nat. Sci. Phila., p. 117, pl. 5, fig. 1 (Lake Woodruff, Volusia Co., Florida; holotype USNM 151038, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 8, pl. 8, fig. 2).

Unio burtchianus S. H. Wright 1897, Nautilus, 10: 137 (St. Marys River, Nassau Co., Florida; lectotype USNM 149653, selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 8, fig. 4, possibly the specimen figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 80, pl. 4, fig. 8).

Unio diazensis S. H. Wright 1897, Nautilus, 11: 5 (Lake Diaz, Volusia Co., Florida; lectotype USNM 149652, selected by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 6).

Unio dispalans B. H. Wright 1899, Nautilus, 13: 50 (Suwannee River, Florida; holotype USNM 159986, figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 80, pl. 1, fig. 9, refigured by Johnson, 1967, Occ. Papers on Moll., 3: 6, pl. 8, fig. 3).

Unio singularis B. H. Wright 1899, Nautilus, 13: 75 (Spring Creek, [a branch of the Flint River], Decatur Co., Georgia; measured holotype USNM 159988, figured by Johnson, 1967, Occ. Papers on Moll., 3: 8, pl. 5, fig. 7).

Elliptio cylindraceus Frierson 1927, Check List North American Naiades, p. 29, new name for *Unio lugubris* Lea, 1838, *non* Say, 1832.

Elliptio maywebbae B. H. Wright 1934, Nautilus, 48: 28; *ibid.* 47, pl. 13, figs. 5–8 (near Seminole Springs [3.4 miles NE Sorrento], 15 miles SE of Eustis [Lake Co.], Florida, refigured by

Johnson, 1967, Occ. Papers on Moll., 3: 7, pl. 10, fig. 3).

Elliptio strigosus (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Description. Shell generally small to medium, seldom reaching over 100 mm in length. Outline variable, subquadrate to subelliptical, sometimes rather pointed. Valves subinflated, subsolid to very solid, inequilateral. Anterior end regularly rounded; posterior end generally biangulate near the base, though sometimes rather produced and pointed. Ventral margin straight or slightly arcuate, sometimes obliquely descending. Dorsal margin slightly curved or almost straight, meeting the obliquely descending posterior margin in a more or less distinct angle. Hinge ligament long and low. Posterior ridge broadly rounded, generally faintly double. Posterior slope flat to slightly concave, sometimes with very faint radial sculpture present. Umbos broad and full but very low, located in the anterior quarter of the shell, their sculpture consisting of several double-looped ridges. Disk surface generally flat, or slightly concave when a slight umbonal-ventral sulcus is present. Periostracum generally fine and shiny, though sometimes heavy and rough, black, brownish black, or yellowish brown or bright yellow, chestnut, often with numerous very fine green rays.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, often of about equal height. Hinge line short and narrow; two long straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one apt to be serrated and chunky, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally purplish, though sometimes salmon, bluish white, or pinkish, posteriorly iridescent.

Length mm	Height mm	Width mm	
98	49	29	Napiers Creek, 6 mi. N McIntyre, Wilkinson Co., Georgia.
81	42	28	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
88	50	30	Canoochee River, 2 mi. N Claxton, Evans Co., Georgia.

Habitat. Found in lakes, ponds, small streams, and large rivers, in nearly every type of substrate. *E. icterina* (Conrad) is sometimes found with *E. complanata* (Lightfoot) and other Unionidae at a given station, but like *complanata*, it is often found alone. In any case, one or the other of these species is generally more abundant than any other unionid at a given station.

Remarks. Elliptio icterina (Conrad), which ranges from the Escambia River system in the Apalachicolan region, east through northern Florida, and north to the White Oak River of North Carolina, is a very variable species and a number of populations have been named, some of them several times over. While some populations are more or less identifiable, there is usually a gradual transition of them between one river system and the next, such that while specimens from extremes of the range bear little resemblance to one another, there appears to be no point at which subspecies can be established. There is often a great deal of ecophenotypic variation, even at what appears to be a single station, the extremes usually connected by intergrades.

In the Apalachicolan region, *E. icterina* can be confused with *E. complanata* (Lightfoot) and *arctata* (Conrad). The latter is a rare species outside of the Alabama River system. It is distinctly and consistently arcuate with compressed valves, whereas *icterina* has a generally straight or curved ventral margin, is bluntly or acutely pointed posteriorly, and when occasionally produced post-basally, the valves are somewhat inflated. *Elliptio icterina*

occurs with *E. complanata* in the Apalachicola River system, and it can be distinguished from *complanata* by its less rhomboid, more elongate, often pointed shape.

The most common shape *E. icterina* takes in the Apalachicolan region is subrhomboidal to subelliptical, sometimes appearing quite pointed posteriorly if the biangulated posterior ridge ends near the medial line. The tendency to be pointed is more prevalent in specimens from the Apalachicolan region than in those from the Southern Atlantic Slope. The similarity of the populations of this species from the Chattahoochee River and the upper Savannah River, first noted in the localities of some of the taxa described by Isaac Lea, further confirms the commingling of the headwaters of these two systems. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 661) under *U. tuomeyi* Lea and by Clench and Turner (1956: 165–169) under *Elliptio strigosus* (Lea).

Noteworthy are the populations in Moccasin Creek of Econfina Creek, Bay Co., Florida, on the Gulf Coast: Black Creek, Florida, St. Marys and Canoochee rivers, Georgia, *all* on the Atlantic Slope; they resemble one another more than they do those from the several intervening river systems. The shells from these rivers tend to be more solid than those from elsewhere, to be more uniformly biangulate posteriorly, and to have a rather characteristic yellowish brown to shiny chestnut periostracum, often with fine dark green rays.

In northern Florida, there is an ecophenotype that lives in lakes and attains much less size than the river one. It has a heavy shell, but tends to be generally oval.

In the Wekiva River and Oklawaha rivers of the St. Johns River system, Florida, there occurs toward the headwaters of the streams and in springs a very thin, compressed, subrhomboidal ecophenotype that ends in a broad biangulation below the medial line, the shells of which tend to be heavier, more inflated, and produced postbasally. This shell form occurs again in abundance in Buckhead Creek of the Ogeechee River system; Brier Creek, of the Savannah River system; *both* Georgia; and the Salkehatchie River of South Carolina; *all* on the Atlantic Slope, which, similar to the Floridian rivers mentioned, are known to be rich in carbonates, Textfigure 4. That the shape of the shell is apparently environmentally controlled is also illustrated by the close resemblance of shells from Magnesia Springs, 3 miles W Hawthorn, Alachua Co., Florida; the headwaters of the Ogeechee River; and Cedar Spring, 2 mi. SE Bamberg, Bamberg Co., South Carolina. Though from widely separated drainage systems, shells from these stations bear a closer resemblance to one another than they do to specimens from other stations in their respective drainage systems. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 641) under *Unio obnubilis* Lea and some of those (1914, 2: 639) under *Unio confertus* Lea.

Especially on the Southern Atlantic Slope, often in the lower parts of rivers, specimens of *E. icterina* tend to be less subrhomboidal than elsewhere, but more elongate and inflated, with a tendency for the ventral margin to be slightly arcuate. The periostracum is often rough, black, and rayless. The shell form just described includes most of the taxa grouped by Simpson (1914, 2: 639) under *Unio confertus* Lea.

On the Atlantic Slope of Georgia, *E. icterina* (Conrad) is most easily confused with *Elliptio complanata* (Lightfoot) with which it is associated at many of the same stations, but *complanata* is quite consistently rhomboidal, and the valves are less inclined to be inflated. The periostracum of *icterina* is sometimes bright yellow or chestnut and is generally more shiny and smooth than that of *complanata*.

Range. Apalachicolan region: Escambia

River system, east to the St. Marys River system, Georgia. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the White Oak River, North Carolina.

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, 2 mi. E St. George; St. Marys River, Traders Hill; Spanish Creek, W Folkston; St. Marys River, 4 mi. SSE Folkston; *all* Charleton Co.

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek, near Macon; Tobesofkee Creek, 5 mi. S Macon; *both* Bibb Co. Mossy Creek, 2 mi. SW Kathleen, Houston Co. Limestone Creek, Brumbrys Mill, 4 mi. NE Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; *both* Pulaski Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 6 mi. NE Cochran, Beckley Co. Alligator Creek, 2 mi. W Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae; Little Ocmulgee River, Lumber City (USNM); *both* Telfair Co.

Oconee River Drainage. *Georgia*: Napiers Creek, 6 mi. N McIntyre, Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin, *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville; Ohoopee River, 2 mi. NE Adrian; *both* Johnson Co. Ohoopee River, 1 mi. E Adrian; Mulepen Creek, 2 mi. E Adrian; Ohoopee River, 1 mi. S Norristown; *all* Emanuel Co.

Little Ohoopee River Drainage. *Georgia:* Little Ohoopee River, 1 mi. E Kite, Johnson Co. Little Ohoopee River, 11 mi. W Swainsboro, Emanuel Co.

Altamaha River Drainage. *Georgia*: [Altamaha River], Hopeton near Darien, McIntosh Co. Frederica, Glynn Co.

Ogeechee River System

Canoochee River Drainage. *Georgia*: Canoochee River, Bulloch Co. Canoochee River, 2 mi. N Claxton, Evans Co. Canoochee River, near mouth, Bryan Co. (MZUM).

Ogeechee River Drainage. *Georgia*: Rocky Comfort Creek, 1 mi. N Louisville; Ogeechee River, 2 mi. S Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; *all* Jefferson Co. Barkeamp Creek, 7 mi. E Midville; Buckhead Creek, 14 mi. W Waynesboro; Buckhead Creek, 4 mi. E Vidotte; Buckhead Creek, 9 mi. SW Waynesboro; Mill Creek, 5 mi. NE Midville; Rocky Creek, 5 mi. SW Waynesboro; *all* Burke Co. Ogeechee River, Scarboro (MZUM); Chew Mill Creek, 8 mi. W Millen; Little Buckhead Creek, 1 mi. N Millen; *all* Jenkins Co.

Savannah River System

Savannah River Drainage. *South Carolina*: Abbeville District. (USNM). Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia*: Savannah River, 0.5 mi. S Augusta; Little Spirit Creek, DeBruce; *both* Richmond Co. *South Carolina:* Lower Three Runs Creek, 8 mi. SW Barnwell, Barnwell Co. Savannah River, 6 mi. W Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia*: Savannah River, 7.5 mi. NE Shell Bluff; Newberry Creek, 2 mi. SE Shell Bluff; Beaverdam Creek, 7 mi. NW Girard; Sweetwater Creek, 2 mi. N Girard; *all* Burke Co. Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Brier Creek, Chalker Bridge, 6 mi. N Waynesboro, Burke Co. Brier Creek, 6 mi. N Sylvania, Screven Co. Rocky Creek, 6 mi. NW Sardis; Miami Branch, 3 mi. NW Sardis; Mill Race, 2 mi. N Sardis; *all* Burke Co. Near [city of] Savannah, Chatham Co. (USNM).

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Salkehatchee River, Broxton Bridge; Whippy Swamp Creek, 2.5 mi. NE Crocketville; *both* Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Snake Swamp Creek [Orangeburg Co.], 6 mi. NE Bamberg, Bamberg Co. N. Fork, Edisto River, Orangeburg, Orangeburg Co. Edisto River, Canadys Landing, 8 mi. SW St. George; Edisto River, Givhans Ferry, 2 mi. NW Givhans; *both* Dorchester Co.

Cooper-Santee River System

Broad River Drainage. *North Carolina*: Green River, 5 mi. ENE Mill Spring, Polk Co.

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. Catawba River; Long Creek; Beaver Creek; *all* Gaston Co. Ashleys Creek; Bissels Pond, Charlotte; *both* Mecklenburg Co.

Wateree River Drainage. *North Carolina:* Wateree River, 2.5 mi. W Camden; Big Pine Tree Creek, 1.5 mi. S Camden; *both* Kershaw Co.

Santee River Drainage. *South Carolina*: Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co. Santee Canal; Cooper River (Conrad); near Charleston; *all* Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Cane Savannah Creek, 4 mi. SW Sumter; Pocotaligo Creek, 3 mi. S Sumter; [right branch] Pocotaligo River, 9 mi. SSE Sumter; Green Swamp Creek, 2.5 mi. W Sumter; *all* Sumter Co. Sammy Swamp Creek, 3 mi. S Paxville, Clarendon Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Yadkin River. Stewarts Pond, Union Co.

Pedee River Drainage. *South Carolina*: Lake Swamp Creek, 7.5 mi. ENE Oates, Darlington Co.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co. *South Carolina:* Ditch, Waccamaw River, 1.25 mi. SE Conway, Horry Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River, Gulf (Lea), Chatham Co.

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co. Livingston Creek, Columbus Co. Ashe River, Pender Co. Cape Fear River.

White Oak River System

White Oak River Drainage. *North Carolina:* White Oak River, Maysville, Onslow Co.

Elliptio (Elliptio) arctata (Conrad)

Plate 10: 4–9

Unio arctatus Conrad 1834, Amer. Jour. Sci., 25: 340, pl. 1, fig. 9 (Black Warrior and Alabama Rivers [Alabama]; figured type not in ANSP. Lectotype, here selected, ANSP 41356, pl. 10, fig. 4, Alabama River, from T. A. Conrad). Conrad, 1834, New Fresh Water Shells United States, p. 36, pl. 5, fig. 4.

Unio strigosus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 198, pl. 9, fig. 9; figured holotype USNM 85890. Lea, 1842, Obs. Unio, 3: 36.

Unio tortivus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 204, pl. 12, fig. 17; USNM 85674 labeled type, does not agree exactly with the figure and is from Lee Co., Georgia, [Flint River drainage]. Lea, 1842, Obs. Unio, 3: 42.

Unio lazarus Lea 1852, Proc. Amer. Philos. Soc., 5: 251 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 11: 259, pl. 14, fig. 9; figured holotype USNM 86155. Lea, 1852, Obs. Unio, 5: 15.

Unio perstriatus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Abbeville District [Savannah River drainage], South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 255, pl. 12, fig. 3; figured holotype USNM 85892. Lea, 1852, Obs. Unio, 5: 11.

Unio gracilentus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 58, pl. 3, fig. 205; figured holotype USNM 85976. Lea, 1862, Obs. Unio, 8: 62.

Unio perlatus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Cape Fear River, Black Rock Landing [= 2 mi. S Kings Bluff, Bladen Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 15, pl. 4, fig. 13; figured holotype USNM 86006. Lea, 1867, Obs. Unio, 11: 19.

Elliptio strigosus (Lea). *partim.* Clench and Turner, 1956, Bull. Florida State Mus., 1: 165.

Description. Shell small, seldom exceeding 60 mm in length. Outline elongated, subelliptical, distinctly arcuate. Valves compressed, subsolid, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded, somewhat biangulate, produced and extending below the base line. Ventral margin arcuate. Dorsal margin slightly curved, usually indistinctly joining the obliquely descending posterior margin. Hinge ligament prominent, located near the middle of the shell. Posterior ridge low and rounded, usually with a faint second ridge above. Posterior slope slightly concave and smooth. Umbos not swollen, nor raised above the hinge line, located in the anterior sixth of the shell, their sculpture consisting of strong ridges. Disk generally slightly concave, caused by a slight umbonal-ventral sulcus. Surface with well-marked but delicate growth lines, often smooth and shiny, becoming darker and duller toward the borders. Periostracum usually greenish or yellowish with green rays over the entire surface becoming wider and more prominent posteriorly, sometimes dark burnt-brown especially on older shells.

Left valve with two low, rather vestigial, somewhat triangular pseudocardinal teeth. Hinge line short and very narrow; two low, short, straight lateral teeth. Right valve with one low but rather chunky pseudocardinal; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct, especially anteriorly. Nacre dirty white or purplish with yellowish splotches, slightly iridescent posteriorly.

Length mm	Height mm	Width mm	
55	22	14	Alabama River, Alabama. Lectotype of *Unio arctatus* Conrad.
56	24	13	Chattahoochee River, Columbus, Muscogee Co., Georgia. Holotype of *Unio strigosus* Lea.
52	23	12	Abbeville District, South Carolina. Holotype of *Unio lazarus* Lea.
49	25	15	Chattahoochee River, Columbus, Muscogee Co., Georgia. Figured type of *Unio tortivus* Lea, after Lea.

Habitat. Lives in rivers near the shore, among and under rocks.

Remarks. On the Atlantic Slope, *Elliptio arctata* (Conrad) is known only from the several type lots, and from a rather large unlocalized series from the Cape Fear River, North Carolina. In spite of the very erratic distributional pattern, there appears to be no morphological difference between the specimens from the Cape Fear River and those from the Alabama River system, where it is most abundant. It becomes distinctly rare eastward.

The thinness and compression of the valves, subelliptical outline, somewhat produced posterior end, and quite consistently arcuate ventral margin distinguish this species from any other *Elliptio* in the Atlantic Slope region.

Range. Alabama-Coosa River system. Apalachicolan region: Escambia River system, east to the Apalachicola River system, but discontinuous. Southern At-

lantic Slope: upper Savannah River system, South Carolina; Catawba River, North Carolina of the Cooper-Santee River system, Lower Cape Fear River system, North Carolina.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Gaston Co. (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Black Rock Landing, 2 mi. S Kings Bluff, Bladen Co. (USNM). Cape Fear River.

Elliptio (*Elliptio*) *lanceolata* (Lea)

Plate 10: 10
Plate 11: 1–6

Obliquaria cuprea Rafinesque 1820, Ann. Gén. Sci. Phys. (Bruxelles), 5: 304, pl. 81, figs. 8, 9 (Le Monongahela et le Potowmak; type not in ANSP [lost]). Ortmann and Walker (1922: 31) have pointed out that this species might be either *E. dilatata* Rafinesque, of the Monongahela River or *producta* Conrad [= *lanceolata* Lea] of the Potomac River. Conrad (1834: 68), as first reviser of this species, referred it to *dilatata*. The type locality is here restricted to the Monongahela River, Pennsylvania, and *O. cuprea* remains a synonym of *E. dilatata* Rafinesque.

Unio lanceolatus Lea 1828, Trans. Amer. Philos. Soc., 3: 266, pl. 3, fig. 2 (Tar River, Tarborough [Edgecombe Co.], North Carolina; figured holotype USNM 85905). Lea, 1834, Obs. Unio, 1: 8.

Unio angustatus Lea 1831, Trans. Amer. Philos. Soc., 4: 114, pl. 17, fig. 43 (Cooper River, South Carolina; figured holotype USNM 85896; Congaree River, South Carolina). Lea, 1834, Obs. Unio, 1: 124.

Unio productus Conrad 1836, Monography Unionidae, no. 3, p. 31, pl. 14, fig. 1 (Savannah River, Augusta [Richmond Co., Georgia]; figured holotype ANSP 41397).

Unio fisherianus Lea 1838, Trans. Amer. Philos. Soc., 6: 8, pl. 4, fig. 8 (Head of Chester River [Kent Co.], Maryland; figured holotype USNM 86022). Lea, 1838, Obs. Unio, 2: 8.

Unio foliculatus Lea 1838, Trans. Amer. Philos. Soc., 6: 38, pl. 11, fig. 33 (Savannah River, [Georgia]; figured holotype USNM 85861). Lea, 1838, Obs. Unio, 2: 38.

Unio duttonianus Lea 1841, Proc. Amer. Philos. Soc., 2: 31 (Ogeechee Canal, Savannah [Chatham Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 236, pl. 22, fig. 50; type not in USNM [lost]. Lea, 1842, Obs. Unio, 3: 74.

Unio sagittiformis Lea 1852, Trans. Amer. Philos. Soc., 10: 277, pl. 22, fig. 35 (Oconee River, near Athens [Clarke Co.], Georgia; figured holotype USNM 85970). Lea, 1852, Obs. Unio, 5: 33.

Unio rostraeformis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Swift Creek, near Macon [Bibb Co.], Georgia). Changed to:

Unio rostriformis Lea 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 64, pl. 10, fig. 46; probable figured holotype USNM 85973. Lea, 1858, Obs. Unio, 6: 64.

Unio extensus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 31 (Dry Creek, near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 68, pl. 12, fig. 49; figured holotype USNM 85995. Lea, 1858, Obs. Unio, 6: 67.

Unio emmonsii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 56, pl. 2, fig. 203; figured holotype USNM 86028. Lea, 1862, Obs. Unio, 8: 60.

Unio naviculoides Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Buckhead Creek, Burke Co.; Macon [Bibb Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 94, pl. 20, fig. 74; figured holotype USNM 86005, from Buckhead Creek, Lea, 1858, Obs. Unio, 6: 94.

Unio maconensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 93, pl. 20, fig. 73; figured holotype USNM 86004. Lea, 1858, Obs. Unio, 6: 93.

Unio hazellhurstianus Lea 1858, Proc. Acad. Nat. Sci. Phila., 9: 166 (Satilla River, Camden Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 211, pl. 26, fig. 92; figured holotype USNM 86009. Lea, 1859, Obs. Unio, 7: 29.

Unio viridulus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Neuse River, near [6 miles E of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6:

10, pl. 3, fig. 7; figured holotype USNM 85908. Lea, 1867, Obs. Unio, 11: 14.

Unio nasutilus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Livingston's Creek, Brunswick Co. [NE corner of Columbus Co., Cape Fear River drainage], North Carolina). Changed to:

Unio nasutulus Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 12, pl. 3, fig. 9; figured holotype USNM 86027. Lea, 1867, Obs. Unio, 11: 16.

Unio attenuatus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 157 (Savannah River; Beaver Creek [few miles E of Bonaire, Ocmulgee River drainage], Houston Co.; *both* Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 41, pl. 14, fig. 38; figured holotype USNM 85974, from Beaver Creek. Lea, 1874, Obs. Unio, 13: 45.

Unio rostellum Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 160 (Macon [Bibb Co.], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 44, pl. 15, fig. 41; figured holotype USNM 85972. Lea, 1874, Obs. Unio, 13: 48.

Unio exactus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Savannah River at Governor Hamilton's [Mansion, 8 mi. S of Hardeeville, Jasper Co., South Carolina], Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 45, pl. 15, fig. 43; figured holotype USNM 85872. Lea, 1874, Obs. Unio, 13: 49.

Unio subcylindraceus Lea 1873, Proc. Acad. Nat. Sci. Phila., 25: 422 (Rocky Creek, near Macon [Bibb Co.]; Carter's Creek [Baldwin Co.]; *both* Georgia). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 58, pl. 20, fig. 57; figured holotype USNM 85863, from Rocky Creek. Lea, 1874, Obs. Unio, 13: 62.

Unio arctior fisheropsis De Gregorio 1914, Il Naturalista Siciliano, 22: 45, pl. 5, figs. 3a-c (Ogeecho [Ogeechee] Canal [Chatham Co.], Georgia; type Palermo Mus., Sicily [not seen]).

Elliptio cupreus (Rafinesque). Ortmann, 1919, Mem. Carnegie Mus., 8: 110, pl. 8, fig. 6.

Elliptio fisherianus (Lea). Ortmann, 1919, Mem. Carnegie Mus., 8: 113, pl. 8, fig. 7.

Description. Shell generally medium throughout most of its range, usually not exceeding 100 mm in length, though reaching over 130 mm in a few localities. Outline elongated trapezoid, or elongated ovate, lance-head shaped, a little over twice as long as high. Valves usually subcompressed, thin to subsolid, occasionally quite solid; inequilateral. Anterior end regularly rounded; posterior end elongated and either sharply or bluntly pointed. The posterior point may occasionally be sharp and turned up above the medial line; sometimes it drops below the medial line, but more generally it is evenly and broadly pointed. Ventral margin gently curved, sometimes almost straight, or a bit arcuate. Dorsal margin straight, forming an indistinct angle with the obliquely descending posterior slope. Hinge ligament rather long and low. Posterior ridge rather broadly rounded or subangular, generally with a secondary ridge above it; the ridges sometimes cause the point to be slightly biangulate. Umbos very low, located in the anterior fourth of the shell, their sculpture consisting of several corrugated, longitudinal ridges. Disk rather flat, or just slightly concave caused by a slight umbonal-ventral sulcus. Surface of the shell with numerous concentric striae. Periostracum fine, subshiny, greenish yellow, olive, often with distinct greenish rays, especially when young, but often becoming rough and brownish or dirty black with age.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, both somewhat triangular; the hinder one may be vestigial. Hinge line rather short and narrow; two long, straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one inclined to be triangular, serrated and chunky, the more anterior one, low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre white, bluish white, pinkish, purplish, posteriorly iridescent.

Length mm	Height mm	Width mm	
134	54	29	Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia.
99	42	20	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.
74	28	14	As above.
68	22	12	As above.

Anatomy. Discussed and figured by Reardon (1929: 11, pl. 5, figs. 1–10). The glochidia are hookless.

Breeding season. Ortmann (1919: 111) found gravid females on May 6, June 3–8, 1912, in the Potomac and James Rivers, Virginia.

Habitat. Lives on sandy bottoms, often found crawling about with much of the shell out of the sand, also found among rocks and in mud, where the current is not too swift.

Remarks. Elliptio lanceolata (Lea), which ranges from the Escambia River system of Florida to the Juniata River of the Susquehanna River system of Pennsylvania, is allied to *Elliptio icterina* (Conrad) and *complanata* (Lightfoot) of the Apalachicolan and Atlantic Slope regions. While *complanata* has a subtrapezoidal shape, *lanceolata* is generally easily distinguished from it by its more elongate, lanceolate shape. Even though the posterior point may be somewhat rounded, it can usually be separated from *complanata* or *icterina* because it is over twice as long as high and because the dorsal and ventral margins are roughly parallel.

On the Atlantic Slope, *E. lanceolata* is most easily confused with *Ligumia nasuta* (Say), which ranges from the James River, Virginia, to the St. Lawrence River, Canada. Anatomically they are quite different, and the shells of *nasuta* show sexual dimorphism and a pattern of green rays that is not found in *lanceolata*. The male shells can be confused, but *nasuta* has a silvery white or cream colored nacre, whereas *lanceolata* may be coppery or purple, with more stumpy hinge teeth. The females of *nasuta* have a peculiar expansion of the lower margin, rendering them easy to distinguish.

Ortmann (1919: 113) separated *fisherianus* from *lanceolata* with some reluctance, on the basis that *fisherianus* was slightly more elongated, with a greater taper to the posterior part of the shell. A few populations of this ecophenotype are found in the northern range of the species and again in the ponds near Wilmington, New Hanover Co., North Carolina.

Reardon (1929: 9) notes that there is no constant distinction either in the anatomy or in the shell morphology. Except for their large size, specimens from Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia, show the same range of variation as do specimens from the Potomac River, Virginia.

There is much local variation in this species throughout its range, and it is easy to see how Issac Lea fell to naming all of the shell forms. The specimens from the type locality and from several other of the rivers in North Carolina are usually small, shiny, and yellowish, without a trace of rays, whereas over the rest of its range, *lanceolata* generally has greenish rays. The species varies considerably as to the ratio of height to length, the sharpness of the posterior point, whether the point is above or below the medial line, and even to the degree of inflation. It can generally be easily separated from any other species of *Elliptio* because it is more than twice as long as high, with the dorsal and ventral margins roughly parallel.

Also found on the Southern Atlantic Slope is *Elliptio shepardiana* (Lea), which is restricted to the Altamaha River system, Georgia, and although it is obviously closely related to *lanceolata,* it differs from *lanceolata* by being over three times as long as high.

In the Suwannee River system of the Apalachicolan region and in Peninsular Florida, *E. lanceolata* is replaced by a closely related species, *Elliptio jayensis* (Lea). While *jayensis* exhibits a range of variation similar to that of *lanceolata,* it is generally smaller, with a tendency to be higher behind. The dorsal and ventral margins are not parallel, and it has more numerous darker green rays.

In the Apalachicolan region, it is often difficult to separate *lanceolata* from *Elliptio icterina* (Conrad), which also some-

times tends to have a lanceolate shell, but even so, these strikingly long shells can generally be separated from any other *Elliptio* by their height to length ratio.

Elliptio lanceolata (Lea) seems to be most abundant on the Atlantic Slope of Georgia. Here and in the Apalachicolan region, individuals reach their greatest size. Specimens from the Carolinas and the north are generally smaller and more delicate.

Range. Apalachicolan region: Escambia River system, east to the Apalachicola River system, but discontinuous; Satilla River system, Georgia. Atlantic Slope: Altamaha River system, Georgia, north to the Juniata River of the Susquehanna River system, Pennsylvania.

Specimens Examined

Satilla River System

Satilla River Drainage. *Georgia*: Satilla River, Camden Co.

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Walnut Creek, 2 mi. E Macon; Rocky Creek (USNM); Swift Creek, 4 mi. E Macon; Tobesofkee Creek, 5 mi. S Macon; *all* Bibb Co. Beaver Creek, E Bonaire (USNM); Mossy Creek, 2 mi. SW Kathleen; Flat Creek, 2 mi. S Perry; *all* Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Big Tuscawhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 7 mi. NE Cochran, Beckley Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, near Athens, Clarke Co. (USNM). Carters Creek, Baldwin Co. (USNM). Napiers Creek, 6 mi. N McIntyre; Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *all* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Turkey Creek, 9 mi. W Dublin; Rocky Creek, 8 mi. W Dudley; *all* Laurens Co. Ochwalkee Creek, 2 mi. E Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville, Johnson Co. Mulepen Creek, 2 mi. E Adrian; Ohoopee River, Norristown; *both* Emanuel Co.

Little Ohoopee River Drainage. *Georgia:* Battleground Creek, 1 mi. N Kite, Johnson Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: [Williamson Swamp Creek] Bartow; Nails Creek, 2 mi. S Bartow; *both* Jefferson Co. Bark Camp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; Buckhead Creek, 9 mi. S Waynesboro; *all* Burke Co. Ogeechee River, bridge 1.5 mi. SW Oliver, Screven Co. (MZUM). Ogeechee River, bridge, 1 mi. E Blitchton; Ogeechee River, Jinks Bridge [Rte. 16]; Dolly Lake, about 1.5 mi. below Kiterlighter Camp; *all* Bryan Co. (*all* MZUM).

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, Augusta, Richmond Co. (ANSP). Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Savannah River, 7.5 mi. NE Shell Bluff; Brier Creek, Chalker Bridge, 6 mi. N Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co. *South Carolina*: Savannah River, 2 mi. SW Millettville (MZUM); Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia:* Savannah River, 8 mi. S Hardeville, Jasper Co. (USNM). Rice fields, near Savannah; Ogeechee Canal, Savannah (Lea); *both* Chatham Co.

Edisto River System

Edisto River Drainage. *South Carolina*: Edisto River [not localized].

Cooper-Santee River System

Cooper River Drainage. *South Carolina:* Cooper River [not localized].

Saluda River Drainage. *South Carolina:* Saluda River, 2.3 mi. above Ware Shoals, Abbeville Co.

Congaree River Drainage. *South Carolina:* Congaree River, Richland Co.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Black River System

Black River Drainage. *South Carolina*: Green Swamp Creek, 2.5 mi. W Sumter; Pocotaligo River, 3 mi. S Sumter; *both* Sumter Co.

Waccamaw River System

Waccamaw River Drainage. *South Carolina*: Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Livingstons Creek, Brunswick Co. (USNM). Wilmington, New Hanover Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Little River, Tarpleys Mill, 2 mi. NE Wendell (5); Little River, 2 mi. WSW Zebulon (6); *both* Wake Co. Neuse River, 6 mi. E Raleigh (USNM).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Tarboro (USNM); Tar River, Old Sparta, 3.5 mi. W Pinetops; *both* Edgecombe Co.

Roanoke River System

Dan River Drainage. *Virginia*: Dan River [Halifax Co.].

Roanoke River Drainage. *Virginia*: Roanoke River, Weldon, Halifax Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, Lexington; [James River], near Natural Bridge; *all* Rockbridge Co. James River, Buchanan, Botetourt Co. James River, Lynchburg, Campbell Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

York River System

South Anna River Drainage. *Virginia*: South Anna River, 1 mi. N. Dabneys, Louisa Co. South Anna River, Gum Tree, Hanover Co.

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, N Unionville, Orange Co. Branch, N Lignum, Culpeper Co.

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Faquier Co. Rappahannock River, Waterloo, Culpeper Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.] 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *West Virginia*: Back Creek, 0.5 mi. E Glengary, Berkeley Co. Shenandoah River, Jefferson Co. *Virginia*: N Fork Shenandoah River, E Woodstock, Shenandoah Co. *Pennsylvania*: Rock Creek, 0.75 mi. N Gettysburg, Adams Co. *Maryland*: Aqueduct Lake Washington Co. Flat Run, Emmitsburg; Monocacy River, 2 mi. W Pleasant; *both* Frederick Co. Potomac River, Great Falls;

Potomac River, below Alexandria; *both* Fairfax Co.

Elliptio (Elliptio) shepardiana (Lea)
Plate 11: 7

Unio shepardianus Lea 1834, Trans. Amer. Philos. Soc., 5: 95, pl. 13, fig. 38 [Altamaha River] Hopeton, near Darien [McIntosh Co.], Georgia; type, not in USNM [lost]; three presumed paratypes MCZ 155568 ex Prof. Shepard. Lea, 1834, Obs. Unio, 1: 207. Simpson, 1914, Cat. Naiades, 2: 698.

Description. Shell often large, reaching over 185 mm in length. Outline extremely elongate, trapezoidal, lance-head shaped, over three times as long as high. Valves subcompressed to subinflated, subsolid, quite inequilateral. Anterior end regularly rounded, usually higher than any other part of the shell; posterior end very elongated and pointed. The point may be at the medial line or below it. Ventral margin almost always arcuate. Dorsal margin roughly parallel to the ventral margin, long and straight, forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament long and low. Posterior ridge rather broadly rounded or subangular, generally with a secondary ridge above it; the ridges sometimes cause the point to be slightly biangulate. Umbos very low, located in the anterior fifth of the shell, their sculpture consisting of several corrugated, longitudinal ridges. Disk surface flat or just slightly concave caused by a slight umbonal-ventral sulcus. Surface of the shell with numerous concentric striae. Periostracum fine, greenish or yellowish, with faint rays when young, becoming rough and brownish or blackish with age.

Left valve with two stumpy pseudocardinal teeth, one in front of the other, both somewhat triangular, the hinder one less high. Hinge line rather short and narrow; two long straight lateral teeth. Right valve with two roughly parallel pseudocardinals, the posterior one inclined to be triangular, serrated, and chunky, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre sometimes bluish white or pinkish but usually purplish or coppery, iridescent posteriorly.

Length mm	Height mm	Width mm	
185	42	26	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
127	29	15	Ocmulgee River, 1 mi. S Lumber City, Telfair Co., Georgia.

Anatomy. Discussed by Lea (1863: 415).

Habitat. Lives in muddy banks, or buried in sand in flowing water.

Remarks. Elliptio shepardiana (Lea) is a singular species and it can be confused with no other one. It is obviously related to *E. lanceolata* (Lea), but differs from it by being over three times as long as high, whereas *lanceolata* is just over twice as long as high. In *shepardiana* the anterior end is the widest part of the shell; it is almost always arcuate, and is consistently pointed. It replaces *E. lanceolata* in the main tributaries of the Altamaha River.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River above Jackson, Butts Co. Big Tucsawhatchee Creek, 6 mi. S Hawkinsville, Pulaski Co. Ocmulgee River, Jacksonville; Ocmulgee River, 1 mi. S Lumber City; *both* Telfair Co. Oconee River Milledgeville, Baldwin Co. Oconee River, 2.5 mi. N Glenwood; Ochwalkee Creek, 2 mi. E Glenwood; *both* Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Montgomery Co. Altamaha River, 10 mi. NE

Surrency, Appling Co. Altamaha River, 11 mi. N Odum; Altamaha River, "Riverside Park," 4 mi. N Jesup; *both* Wayne Co. Altamaha River, 3 mi. NE Everett City, Glynn Co. Altamaha River, near Fort Barrington; Penhollaway Creek, 5 mi. S Fort Barrington; Altamaha River, Hopeton, near Darien; *all* McIntosh Co.

Genus *Uniomerus* Conrad

Uniomerus Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 268. Species listed: *U. declivis* Say, *camptodon* Say, *subcroceus* Conrad, *sayii* Ward, *rivularis* Conrad, *porrectus* Conrad, *symmetricus* Lea, *excultus* Conrad.
Conrad, 1854, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 296.

Type species, *Unio tetralasmus* Say. Subsequent designation, Simpson, 1900, Proc. United States Natl. Mus., 22: 739. Since *U. excultus* Conrad is included in Simpson's synonymy of *U. tetralasmus*, the subsequent selection of the former by Clench and Turner, 1956, Bull. Florida State Mus., 1: 176, is invalid under Article 69 (a) (iv) of the Int. Code Zool. Nomen. (1964). Ortmann, 1912a, Ann. Carnegie Mus., 8: 272.

Frierson (1927: 34–35) lists a number of species and subspecies under *Uniomerus*. Like *Elliptio*, *Uniomerus* has a wide range of environmental tolerance, and while there are a number of ecophenotypes, the genus appears to be monotypic.

Uniomerus tetralasmus (Say)
Plate 12: 1–6

Unio tetralasmus Say, [September] 1831, American Conchology, no. 3 [no pagination] pl. 23 (Bayou St. John [not located] near New Orleans, Louisiana; type not in ANSP [lost]).

Unio obesus Lea 1831, Trans. Amer. Philos. Soc., 4: 96, 108, pl. 13, fig. 26 (York River, Virginia [corrected to Georgia; Maj. Leconte on p. 108]; figured holotype USNM 85366, labeled, "Little Ogeechee River [Hancock Co.], Georgia; Maj. Leconte"). Lea, 1834, Obs. Unio, 1: 106, 118. Clench and Turner, 1956, Bull. Florida State Mus., 1: 178, did not see the type, which has the corrected locality written on it, and unfortunately restricted the type locality to Columbus, Georgia.
Lea, 1854 (Proc. Acad. Nat. Sci. Phila., 7: 243), claimed that this description appeared during the latter part of 1831. It was reported on in 1832, (Jan.-March number of: Amer. Jour. Sci., 22: 169 [probably appeared in April]). There is no way to be sure which name has priority, but Say's name is certainly better known, and it is given primary status here without equivocation.

Unio declivis Say 1831 [1832], Transylvania Jour. Med., 4: 527 (Bayou Teche, Louisiana). Say, 1832, American Conchology, no. 4 [no pagination], pl. 35; three syntypes ANSP 41698 from Mr. Barabino, all smaller than figured type.

Unio camptodon Say 1832, American Conchology, no. 5 [no pagination], pl. 42 (opposite to New Orleans [Jefferson Parish, Louisiana], in ponds; type not in ANSP [lost]).

Unio geometricus Lea 1832, Trans. Amer. Philos. Soc., 5: 38, pl. 4, fig. 10 (Bayou Teche, Louisiana; figured holotype USNM 85712) Lea, 1834, Obs. Unio, 1: 150.

Unio blandingianus Lea 1834, Trans. Amer. Philos. Soc., 5: 101, pl. 15, fig. 44 (St. Johns River, Florida; figured holotype USNM 85715). Lea, 1834, Obs. Unio, 1: 213.

Unio declivis Conrad 1836 *non* Say. See under: *Unio rivularis* Conrad, 1853.

Unio excultus Conrad, 1838, Monography Unionidae, no. 11, p. 99, pl. 55, fig. 1 (New Orleans [Orleans Parish], Louisiana; type ANSP 20427 [lost]).

Unio sayii Ward 1839, [*in* Tappan], Amer. Jour. Sci., 35: 268, pl. 3, fig. 1 (Walnut Creek and Ohio Canal, near Circleville [Pickaway Co.], Ohio; type [location unknown]).

Unio paralellus [*sic*] Conrad 1841, Proc. Acad. Nat. Sci. Phila., 1: 20 *non* Sowerby 1840. Changed to:

Unio porrectus Conrad 1845, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 296, pl. 26, fig. 7 ([Pearl River] Jackson [Hinds Co.], Mississippi; figured holotype ANSP 42847).

Unio buddianus Lea 1843, Desc. Twelve Uniones (Lake George and Lake Monroe, Florida). Lea, 1845, Trans. Amer. Philos. Soc., 9: 277, pl. 40, fig. 5; figured holotype USNM 85606, from Lake George. Lea, 1848, Obs. Unio, 4: 35.

Unio symmetricus Lea 1845, Trans. Amer. Philos. Soc., 10: 73, pl. 4, fig. 11 (Red River, Alexandria [Rapides Parish] Louisiana; figured holotype USNM 85604). Lea, 1848, Obs. Unio, 4: 47.

Unio paludicolus Gould 1845, Proc. Boston Soc. Nat. Hist., 2: 53 (Florida Everglades; lectotype MCZ 169278, selected by Johnson, 1964, Bull. United States Natl. Mus., 239: 121, pl. 31, fig. 3).

Unio ineptus Lea 1852, Trans. Amer. Philos. Soc., 10: 261, pl. 15, fig. 12 (Abbeville District [Savannah River drainage], South Carolina;

figured holotype USNM 85326). Lea, 1852, Obs. Unio, 5: 17.

Unio hebes Lea 1852, Trans. Amer. Philos. Soc., 10: 267, pl. 18, fig. 21 (Oconee River, near Athens [Clarke Co.], Georgia; figured holotype USNM 85383). Lea, 1852, Obs. Unio, 5: 23.

Unio rivularis Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 257. New name for *Unio declivis* Conrad 1836 *non* Say 1831, *in* Monography Unionidae, no. 5, p. 45, pl. 23, fig. 1 (small creek in Green Co., Alabama; figured holotype ANSP 42852).

Unio paludicolor Conrad 1853, Proc. Acad. Nat. Sci. Phila., 6: 254. Error for *U. paludicolus* Gould.

Unio subcroceus Conrad 1854, Jour. Acad. Nat. Sci. Phila., ser. 2, 2: 297, pl. 27, fig. 1 (one of the tributaries to Canadian River, Arkansas; type not in ANSP [lost]).

Unio manubius Gould 1855, Proc. Boston Soc. Nat. Hist., 5: 229 (Chihuahua, 60 mi. from Camp Ringgold = Río Agualeguas, 3 mi. NE General Trevino, Nuevo Leon [State, Mexico], *teste* Taylor, 1967, Veliger, 10: 154; holotype MCZ 169447, figured by Johnson, 1964, Bull. United States Natl. Mus., 239: 108, pl. 32, fig. 5).

Unio columbensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 31 (Creeks near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 75, pl. 14, fig. 55; figured holotype USNM 85360. Lea, 1858, Obs. Unio, 6: 75.

Unio jamesianus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 ([Pearl River] Jackson [Hinds Co.], Mississippi). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 53, pl. 6, fig. 35; figured holotype USNM 85365). Lea, 1858, Obs. Unio, 6: 52.

Unio plantii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 171 (Flint River, near Macon [Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 192, pl. 21, fig. 76; figured holotype USNM 85005. Lea, 1859, Obs. Unio, 7: 10. [Known only from the holotype, which is a pathological specimen].

Unio cicur Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 39 (Little Ocmulgee River, Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 93, pl. 13, fig. 241; figured holotype USNM 85532. Lea, 1862, Obs. Unio, 8: 97.

Unio squalidus Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 192 (Neuse River, near Raleigh [Wake Co.]; Roanoke River, near Weldon [Halifax Co.]; Deep River; *all* North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 22, pl. 7, fig. 20; figured holotype USNM 85376, from Roanoke River. Lea, 1867, Obs. Unio, 11: 26.

Unio electrinus Reeve 1865, Conch. Iconica, 16, *Unio*, pl. 25, fig. 121 (Hab. ? Cuming colln; type, British Museum (Nat. Hist.) [lost]).

Unio bisselianus Lea 1867, Proc. Acad. Nat. Sci. Phila., 15: 81 (Bissels Pond, Charlotte [Mecklenburg Co.], North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 277, pl. 37, fig. 90; figured holotype USNM 85373. Lea, 1869, Obs. Unio, 12: 37.

Unio jewettii Lea 1867, Proc. Acad. Nat. Sci. Phila., 11: 81 (sink of Noonan's [Newnans] Lake [Alachua Co.], Florida). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 276, pl. 37, fig. 89; figured holotype USNM 85374. Lea, 1869, Obs. Unio, 12: 36.

Unio rivicolus Conrad 1868, Amer. Jour. Conch., 4: 280, pl. 18, fig. 4 (brook near Tampa [Hillsborough Co.], Florida; figured holotype ANSP 41411).

Unio pawensis Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Paw Creek [Mecklenburg Co.], Beaver Co. [= Creek, Gaston Co.], Catawba Run [Gaston and Mecklenburg Cos.]). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 302, pl. 45, fig. 114; figured holotype USNM 85380, labeled, "Beaver Creek, [into ?] Catawba Run, North Carolina." Lea, 1869, Obs. Unio, 12: 62.

Uniomerus obesus (Lea). Clench and Turner, 1956, Bull. Florida State Mus., 1: 177, pl. 5, fig. 2.

Description. Shell medium to large, reaching 114 mm in length. Outline rhomboid or long rhomboid. Valves subinflated or inflated, subsolid. Anterior end regularly rounded or slightly truncated; posterior end usually somewhat produced. Ventral margin slightly incurved. Dorsal margin slightly curved, generally forming a sharp angle with the almost straight posterior margin. Hinge ligament long and narrow, located posteriorly of the umbos. Posterior ridge rounded, ending in a point or feeble biangulation at the base of the shell, sometimes rendering older specimens a bit arcuate. Posterior slope often with two radial sulci. Umbos low to slightly elevated, located in the anterior quarter of the shell, their sculpture consisting of five or six heavy ridges that form a rounded angle on the posterior ridge, in front of which they tend to be corrugated. Periostracum generally black and slightly roughened, but with a satiny

sheen over most of the surface. Sometimes the surface is smooth and shiny, especially in the umbonal area, and may then be brownish yellow or yellowish mixed with green, not rayed.

Left valve with two ragged, subequal pseudocardinal teeth and two straight lateral teeth. Right valve with one triangular pseudocardinal often with a vestigial tooth above it; one lateral tooth. Beak cavities compressed, but with several muscle scars; anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct. Nacre white, bluish white or pinkish to lurid purple.

Length mm	Height mm	Width mm	
114	61	39	Ogeechee River, Bartow, Jefferson Co., Georgia.
102	59	36	Little Cedar Creek, 1 mi. E Wrightsville, Jefferson Co., Georgia.
70	40	29	Richardson Creek, 2 mi. NE Thrift, Jenkins Co., Georgia.

Anatomy. Discussed by Lea (1863: 404).

Habitat. Generally lives in smaller streams and ponds on muddy bottoms, where it may be locally abundant. Sometimes found in sand with *Elliptio complanata* (Lightfoot) in larger Southern Atlantic Slope rivers, but in this habitat it is relatively scarce.

Remarks. In the Apalachicolan and Southern Atlantic Slope regions, *Uniomerus tetralasmus* (Say) can be confused with both *Elliptio complanata* (Lightfoot) and *E. icterina* (Conrad). In general, *tetralasmus* is more inflated than either of them, is proportionately higher, more acutely angular where the dorsal margin meets the posterior one, and very often has a satiny periostracum. The yellowish brown, unrayed periostracum and the bluish white or pinkish nacre of *tetralasmus* are distinct from the brown, often rayed periostracum and the dark purplish bronze nacre of *complanata.* The periostracum of *icterina* is sometimes bright yellow or chestnut, but like *complanata,* is generally rayed, though often but faintly, whereas *tetralasmus* scarcely ever appears rayed.

Uniomerus tetralasmus (Say) is generally common and abundant throughout the Apalachicolan region, Peninsular Florida, and in the Southern Atlantic Slope rivers of Georgia. It becomes noticeably scarce in the Carolinas. The periostracum is more inclined to be smooth on individuals from this northern end of the range.

Range. Interior Basin: Mississippi drainage generally, north to about latitude 40 degrees, Ohio River. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Rio Grande River system, Texas, east to the Suwannee River system, Florida. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, north to the Nottoway River of the Chowan River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Swift Creek, SE Macon, Bibb Co. Mossy Creek, 3.5 mi. SW Kathleen, Houston Co. Tucsawhatchee [= Big] Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. WSW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Brushy Creek, 8 mi. NW Abbeville, Wilcox Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald, Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 6 mi. NE Cochran, Bleckley Co. Alligator Creek, 2.5 mi. SW Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, near Athens, Clarke Co. (USNM). Black Creek, 7 mi. N McIntyre; Napiers Creek, 6 mi. N McIntyre; Ochee Creek, about 5 mi. SE Toomsboro; *all* Wilkinson Co. Rocky Creek, 6 mi. E Dudley; Turkey Creek, 6 mi. W Dublin; *both* Laurens Co. Ochwalkee Creek, 2 mi. E Glenwood, Wheeler Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Tennible, Washington Co. Little Ohoopee River, 10 mi. NE Wrightsville; Little Cedar Creek, 1 mi. E Wrightsville; Big Cedar Creek, 1 mi. SE Wrightsville; outlet of Rollins Pond, 2 mi. SE Wrightsville; Battleground Creek, 1 mi. N Kite; Dry Creek, 9 mi. NW Adrian; *all* Johnson Co. Pendleton Creek, 8 mi. N Soperton, Treutlen Co. Mulepen Creek, 2 mi. E Adrian; Yam Grande Creek, 3 mi. W Swainsboro; Little Ohoopee River, 6 mi. SW Swainsboro; *all* Emanuel Co.

Altamaha River Drainage. *Georgia*: Hopeton, near Darien, McIntosh Co. Brunswick, Glynn Co.

Ogeechee River System

Canoochee River Drainage. *Georgia*: Rocky Creek, 1.5 mi. E Swainsboro; Canoochee River, 4 mi. E Swainsboro; Little Canoochee Creek, 6 mi. E Swainsboro; *all* Emanuel Co. Little Lotts Creek, 2 mi. SE Statesboro; Lotts Creek, 7 mi. SW Statesboro; *both* Bulloch Co.

Ogeechee River Drainage. *Georgia*: Little Ogeechee River [Hancock Co.] (USNM). Ogeechee River, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; *all* Jefferson Co. Mill Creek, 5 mi. E Midville; Barkcamp Creek, 7 mi. E Midville; Barkcamp Creek, 9 mi. SW Waynesboro; *all* Burke Co. Spring, Ogeechee River, 1 mi. S Millen; Richardson Creek, 2 mi. NE Thrift; *both* Jenkins Co. Ogeechee River, Flat Ford Landing (MZUM); Dolly Lake, about 1.5 mi. below Kiterlighter Camp (MZUM); *both* Bryan Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM), Turkey Creek, 7 mi. NW Edgefield, Edgefield Co. *Georgia:* Beaverdam Creek, 7 mi. NW Girard; outlet of Waynesboro Lake, Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co. Brier Creek, 6 mi. N Sylvania, Screven Co. Savannah River, Atomic Energy Plant, 25 mi. S Augusta (ANSP). *South Carolina*: Savannah River, 2 mi. SW Millettville (ANSP); Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *both* Allendale Co. Mouth of Vermezobre Creek, Savannah Wildlife Reservation, Jasper Co. (MZUM). *Georgia*: Pond near Savannah, Chatham Co.

Combahee River System

Salkehatchie River Drainage. *South Carolina:* Lemon Creek, 5 mi. W Smoaks, Colleton Co.

Edisto River System

Edisto River Drainage. *South Carolina:* 20 mi. W Charleston, Charleston Co. Edisto River [not localized].

Cooper-Santee River System

Cooper River Drainage. *South Carolina:* Cooper River (USNM).

Catawba River Drainage. *North Carolina:* Beaver Creek, Gaston Co. Paw Creek; Irwins Creek; Bissels Pond, Charlotte; Elias Pond, 10 mi. from Charlotte; *all* Mecklenburg Co.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden; Big Pine Tree Creek, 1.5 mi. S Camden; *both* Kershaw Co.

Santee River Drainage. *South Carolina:* Green Swamp Creek, 2.5 mi. W Sumter, Sumter Co. Poplar Creek, Schulers Fish Pond, near Santee State Park, Orangeburg Co. Santee River, Cross, Berkeley Co.

Black River System

Black River Drainage. *South Carolina*: Cowpen Swamp, 11 mi. NE Sumter, Sumter Co.

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Yadkin River Drainage. *North Carolina:* Yadkin River.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw (USNM); drainage canal beside Lake Waccamaw, 1 mi. NNW Dupree Landing; *both* Columbus Co. *South Carolina:* Waccamaw River, Wachesaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River (USNM).

Cape Fear River Drainage. *North Carolina:* Rocky River, Chatham Co. 11 mi. N Sanford, Lee Co. Stream below Greenfield Mill Pond, Wilmington, New Hanover Co. (ANSP).

Neuse River System

Neuse River Drainage. *North Carolina:* Neuse River, near Raleigh, Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Sandy Creek, Franklin Co. Fishing Creek, 4 mi. E Leggett; Tar River, Tarboro; *both* Edgecombe Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, near Weldon, Halifax Co. (USNM).

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River.

Subfamily **Anodontinae** (Swainson 1840) Ortmann 1910

Genus *Lasmigona* Rafinesque

Subgenus *Lasmigona s.s.* Rafinesque

Lasmigona Rafinesque 1831, Continuation of Monog. Bivalve Shells of River Ohio (Phila.), p. 4. Species listed: *Alasmidonta marginata* Say, *A. costata* Rafinesque.

Type species, *Alasmidonta costata* Rafinesque. Subsequent designation, Simpson 1900, Proc. United States Natl. Mus., 22: 664.

Symphynota Simpson 1900, Proc. United States Natl. Mus., 22: 662.

Type species, *Symphynota compressa* Lea, original designation, *non Symphynota* Lea 1829, the type species of which is *Unio alata* Say. Original designation.

There is only one species in *Lasmigona s. s., L. costata* (Rafinesque), which is found in the Interior Basin and the upper St. Lawrence River system. In addition to the subgenera discussed here are *Alasminota* Ortmann (*Sulcularia* Rafinesque is not identifiable, *teste* Ortmann and Walker, 1922: 36) and *Pterosyna* Rafinesque. They do not occur on the Atlantic Slope, but belong to the Interior Basin.

Subgenus *Platynaias* Walker

Symphynota Simpson 1900, Proc. United States Natl. Mus., 22: 662. [*non*] Lea. (See under *Lasmigona*, above.)

Platynaias Walker 1918, Occ. Pap. Mus. Zool., Univ. Mich., 49: 2.

Type species, *Symphynota compressa* Lea, original designation.

Platynaias probably contains only two, probably allopatric species, *L. compressa* (Lea) (Ortmann 1919: 116, pl. 9, figs. 1, 2 as *L. viridis* Rafinesque), which is found in the Interior Basin, Hudson Bay; Upper Mississippi, Ohio, and St. Lawrence River systems from Saskatchewan and Nebraska to Vermont; extending into the Hudson River on the Atlantic Slope; and *L. subviridis* (Conrad), which is primarily a species of the Atlantic Slope, but which extends into the Lake Ontario drainage. Most of the other taxa listed under this subgenus by Frierson (1927: 20, 21) are included elsewhere in this paper in synonymy, save for *L. neglecta* (Lea) and *L. quadrata* (Lea) which are out of the scope of this paper.

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Plate 12: 7–9
Plate 13: 1

Unio subviridis Conrad 1835, New Fresh Water Shells United States; appendix, p. 4, pl. 9, fig. 1 (Schuylkill River; Juniata River [Blair Co.];

figured holotype ANSP 2105 [lost]; creeks in Lancaster Co.; [*all* Pennsylvania]).

Unio viridis Conrad 1836, Monography Unionidae, no. 4, p. 35, pl. 17, fig. 1, *non* Rafinesque 1820.

Unio tappanianus Lea 1838, Trans. Amer. Philos. Soc., 6: 62, pl. 17, fig. 55 ([Frankstown Branch], Juniata River, near Hollidaysburg [Blair Co.]; figured holotype USNM 85240; Schuylkill [River]; and a small stream near Lancaster; [*all* Pennsylvania]). Lea, 1838, Obs. Unio, 2: 62.

Unio hyalinus Lea 1845, Proc. Amer. Philos. Soc., 4: 164 ([James River drainage], Richmond [Henrico Co.], Virginia). Lea, 1848, Trans. Amer. Philos. Soc., 10: 69, pl. 2, fig. 4; figured holotype USNM 86131. Lea, 1848, Obs. Unio, 4: 43.

Unio decoratus Lea 1852, Trans. Amer. Philos. Soc., 10: 257, pl. 13, fig. 6 (Abbeville District [Savannah River drainage] South Carolina; figured holotype USNM 83972). Lea, 1852, Obs. Unio, 4: 43.

Unio pygmaeus Lea 1852, Proc. Amer. Philos. Soc., 5: 52 (Abbeville District [Savannah River drainage] South Carolina). Lea, 1852, Trans. Amer. Philos. Soc., 10: 262, pl. 15, fig. 14; figured holotype USNM 85240. Lea, 1852, Obs. Unio, 5: 18.

Unio charlottensis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 191 ([Sugar Creek], near Charlotte, Mecklenburg Co., North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 8, pl. 2, fig. 5; figured holotype USNM 85402. Lea, 1867, Obs. Unio, 11: 12.

Unio pertenuis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Neuse River, near [6 mi. E of] Raleigh [Wake Co.], North Carolina). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 8, pl. 2, fig. 4; figured holotype USNM 86139. Lea, 1867, Obs. Unio, 11: 12.

Unio insolidus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 159 (Abbeville District [Savannah River drainage] South Carolina; Fredericksburg [Spotsylvania Co.], Virginia; Irwin's Creek, Mecklenburg Co., North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 40, pl. 13, fig. 37; figured holotype USNM 83974 from Irwin's Creek, Lea, 1874, Obs. Unio, 13: 44.

Symphynota viridis (Conrad). Simpson, 1914, Cat. Naiades, 1: 484.

Symphynota charlottensis (Lea). Simpson, 1914, Cat. Naiades, 1: 484.

Symphynota decorata (Lea). Simpson, 1914, Cat. Naiades, 1: 486.

Unio pygmaeus (Lea). Simpson, 1914, Cat. Naiades, 2: 649.

Lasmigona (*Platynaias*) *subviridis* (Conrad). Ortmann, 1919, Mem. Carnegie Mus., 8: 121, pl. 9, figs. 3, 4. Ortmann and Walker, 1922, Occ. Pap. Mus. Zool. Univ. Michigan, no. 112, p. 35. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 32, fig. 31.

Description. Shell generally small, seldom reaching over 55 mm in length. Outline subrhomboid or subovate. Valves subcompressed to slightly inflated, subsolid. Anterior end regularly rounded; posterior end more broadly rounded and biangulate near the base. Ventral margin almost straight or slightly curved. Dorsal margin straight, sometimes forming a winglike angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge low, but double, ending near the base of the shell in a slight biangulation. Posterior slope sometimes slightly concave above the upper ridge. Umbos elevated above the hinge line, located anterior to the middle of the shell, their sculpture consisting of about four subnodulous bars, the first two subconcentric, the others deeply double-looped, anterior loops rounded, posterior ones angular with a few radial threads behind. The disk is smooth or slightly roughened by growth rests; periostracum yellowish or brownish green, occasionally olivaceous, subshining to dull, usually faintly rayed over the entire surface, darker on the posterior slope.

Hinge teeth well developed but rather delicate. Left valve with two lamellate, pseudocardinals that are directed forward and almost parallel to the hinge with a rudimentary interdental projection which fits into an interdental groove in the right valve; two long, straight, thin, lateral teeth. Right valve with one long pseudocardinal, directed forward, almost parallel to the hinge line; interdentum wide; one thin lateral tooth. Beak cavities shallow, containing dorsal muscle scars. Anterior adductor muscle scars distinct, posterior ones less so. Pallial line distinct anteriorly, where the shell may be slightly thickened.

Nacre bluish white and iridescent, sometimes pinkish, especially toward the umbonal cavities.

Length mm	Height mm	Width mm	
60	37	19	Abbeville District [Savannah River drainage], South Carolina. Holotype of *Unio decoratus* Lea.
30	18	11	As above. Holotype of *Unio pygmaeus* Lea.
116	56	38	Pfeiffers Pond, Charlotte, Mecklenburg Co., North Carolina (ANSP).
117	59	29	*Lasmigona compressa* (Lea). Small brook, Middlebury, Addison Co., Vermont.

Anatomy. Discussed by Ortmann (1911: 283). Glochidia are subtriangular, almost semicircular, with hooks. They measure 0.36 mm in length, 0.30 mm in height. The host fish is not known.

Breeding season. This hermaphroditic species is bradytictic, the breeding season beginning in August and lasting until June (Ortmann, 1919: 122).

Habitat. Usually found in gravel or sandy bottoms in medium or small streams, as well as canals and the pond areas of streams; seems to avoid large rivers.

Remarks. With its lamellate pseudocardinal teeth and characteristic rudimentary interdental projection in the left valve, *Lasmigona subviridis* (Conrad) is not confused with any other Atlantic Slope species, except in New York, where its distribution overlaps that of *Lasmigona compressa* (Lea) in the lower St. Lawrence and Hudson river systems. *L. compressa,* which is found abundantly in the Ohio-Mississippi drainage of the Interior Basin, has a rather heavy, compressed, trapezoidal shell, and the left valve has a well-developed interdental projection. *L. subviridis* has almost invariably a smaller, thinner, more delicate shell which is more inflated (see comparative measurements, above), and the interdental projection is rudimentary.

Ortmann (1919: 123) calls attention to some specimens of *L. subviridis* from Conococheague Creek, Greencastle, Franklin Co., Pennsylvania, remarkable for their large size. The largest one measured 63 mm in length, 38 mm in height, and 26 mm in width. Lea described a single giant specimen of this species under the name *Unio charlottensis,* from Sugar Creek, near Charlotte, Mecklenburg Co., North Carolina, part of the Catawba River drainage of the upper Cooper-Santee River system, which measured 112 mm in length. During the last century, a few additional giant specimens, as well as a number of smaller ones, were collected in Pfeiffers Pond, Charlotte, Mecklenburg Co., North Carolina, by C. M. Wheatley (ANSP and MCZ). The original label on the lot in the Academy of Natural Sciences of Philadelphia (ca. 1900) states that, "the pond from which they were taken has long since been filled in."

Ortmann (1913a: 371; 1919: 124) found *L. subviridis* to be especially abundant on the west side of the Alleghenian divide in the Greenbrier and New rivers of the upper Kanawha drainage in Virginia and West Virginia, where he suggested this species originated.

Range. Interior Basin: New and Greenbrier rivers of the upper Kanawha River drainage, Virginia and West Virginia. Atlantic Slope: upper Savannah River system, South Carolina; north to the Hudson River system, westward through the Mohawk River and Erie [now New York State Barge] Canal to the Genesee River; *all* New York.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Irwins Creek (MZUM); Sugar Creek,

near Charlotte (USNM); Pfeiffers Pond, Charlotte; *all* Mecklenburg Co. [Ten Mile Creek], Wolfsville [7 mi. W Monroe], Union Co. (MZUM).

Pedee River System

Yadkin River Drainage. *North Carolina:* Crosiers Branch, Cabarrus Co. (ANSP).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Kinnon, Cumberland Co. (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Flat River, 2.5 mi. S Mt. Tirzah, Person Co. (80). Flat River, 2.3 mi. ENE Rougemont, Durham Co. (78). Eno River, 1.75 mi. ESE Hillsboro Center, Orange Co. (117). Neuse River, 9.5 mi. ENE Durham, Durham Co. (62). Neuse River, 5 mi. NNW Bayleaf (56); Neuse River, Falls (50); Neuse River, 5.75 mi. E Raleigh (45); Neuse River, 3 mi. S Milburnie (33); Stirrup Iron Creek, 2 mi. NE Morrisville (43); Swift Creek, 3 mi. SSW Garner (20); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co. Neuse River, 3.5 mi. NNE Smithfield, Johnston Co. (25).

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Providence, Granville Co. (MZUM). Tar River, 2 mi. W Springhope, Nash Co.

Roanoke River System

Roanoke River Drainage. *Virginia*: Stone River, Clarksville, Mecklenburg Co. (MZUM).

James River System

Appomattox River Drainage. *Virginia*: Appomattox River, Petersburg, Dinwiddie Co. (MZUM).

James River Drainage. *Virginia*: North River, Buena Vista, Rockbridge Co. (Ortmann, 1919: 124). Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co. [James River], Richmond, Henrico Co. (Lea).

York River System

North Anna River Drainage. *Virginia*: Church River, Orange Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, 3 mi. N Orange, Orange Co. Rapidan River, Rapidan, Culpeper Co. (Ortmann, 1919: 124).

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Fauquier Co. (Ortmann, 1919: 124). [Rappahannock River], Fredericksburg, Spotsylvania Co. (Lea).

Potomac River System

Potomac River Drainage. *West Virginia:* Sleepy Creek, 8 mi. E Berkeley Springs, Morgan Co. (MZUM). *Virginia:* S. Fork, Shenandoah River, Elkton, Rockingham Co. (Ortmann, 1919: 124). *West Virginia:* S. Fork, Shenandoah River, Harpers Ferry, Jefferson Co. (Ortmann, 1919: 124). *Virginia:* Potomac River, 5 mi. S Lucketts, Loudoun Co. Potomac River, Great Falls County Park, Fairfax Co. (USNM).

Genus *Alasmidonta* Say
Subgenus *Prolasmidonta* Ortmann

Prolasmidonta Ortmann 1914, Nautilus, 28: 44. Type species, *Unio heterodon* Lea, original designation. This subgenus is monotypic.

Alasmidonta heterodon (Lea) is restricted to the Atlantic Slope region. The general shape and the distinct posterior ridge give the shell the unmistakable look of an *Alasmidonta,* but it is not close to the other members of the genus. There are two lateral teeth in the right valve and one in the left which is the reverse arrangement

of these teeth in all other Atlantic Slope Unionidae.

Alasmidonta (Prolasmidonta) heterodon (Lea)

Plate 13: 2

Unio heterodon Lea 1830, Trans. Amer. Philos. Soc., 3: 428, pl. 8, fig. 11 (Schuylkill [River] and Derby Creek [mostly in Delaware Co.], Pennsylvania; figured type, belonged to Mr. Mason, not in USNM or ANSP [presumed lost]. Lea mentions specimens in possession of T. A. Conrad, now ANSP 41004, 41005). Lea, 1834, Obs. Unio, 1: 42.

Alasmidonta heterodon (Lea) 1914, Simpson, Cat. Naiades, 1: 499.

Alasmidonta (Prolasmidonta) heterodon (Lea). Ortmann, 1919, Mem. Carnegie Mus., 8: 173, pl. 12, figs. 1, 2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 24, fig. 35.

Description. Shell small, generally from 30 to 45 mm, seldom reaching more than 50 mm in length. Outline subrhomboidal or subtrapezoidal, sometimes more or less elongate. Valves rather flat, though females are somewhat swollen in the region of the posterior ridge, thin but strong. Anterior end regularly rounded; posterior end somewhat produced and angular. Ventral margin straight or slightly arcuate. Dorsal margin short and straight, almost always forming a sharp angle with the obliquely descending posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge distinct though broadly rounded, sometimes almost angular in females, usually ending in a broad point near the base. Posterior slope flat, or slightly concave, with one or two fine radiating lines. Umbos somewhat inflated but not very prominent, located slightly anterior to the middle of the shell, their sculpture consisting of three or four, sometimes five, bars, the first two concentric, the others with a distinct angle on the posterior ridge in front of which is a shallow sinus. The bars are rather heavy; the sinus does not assume the shape of a re-entering angle, and the sculpture can not be regarded as double-looped. The disk is smooth; the periostracum is greenish olive to brownish. In addition to indistinct concentric bands of lighter and darker green, there are often obscure green rays which are occasionally sharp and well defined.

Hinge teeth delicate. Left valve with two lamellate pseudocardinal teeth which are parallel to the hinge, the anterior one sometimes rudimentary; an interdental tooth that may be well developed and isolated or connected with the posterior pseudocardinal; one lateral tooth. Right valve with two compressed crenulated pseudocardinals, the more anterior one often rudimentary; interdentum narrow and short; two delicate lateral teeth, the upper one often partially rudimentary. Beak cavities shallow, containing dorsal muscle scars. Anterior adductor muscle scars distinct, posterior ones less so. Pallial line distinct anteriorly only. Nacre bluish or silvery white, often cream colored or yellowish toward the umbonal cavities.

Sexual differences are visible in the shell. In general the male shell is compressed, ovate, and elongate, with the ventral margin curved, the posterior ridge not sharp, and the posterior slope not truncate, whereas the female shell is swollen in the region of the posterior ridge, rendering the posterior slope truncate, the outline of the shell more trapezoidal, and the ventral margin slightly concave.

Length mm	Height mm	Width mm	
52	26	17	[Ten Mile River], Mixville, Cheshire, New Haven Co., Connecticut. Male.
40	23	16	Neuse River, Pooles Bridge, Wake Co., North Carolina. Male.
38	22	18	Little River, 2 mi. NE Wendell, Wake Co., North Carolina. Female.

Anatomy. Discussed by Lea (1863: 442) and Ortmann (1911: 295). Glochidia are subtriangular with strong hooks. They measure 0.30 mm in length, 0.25 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 174) reports gravid females having been taken in February and April. It is bradytictic.

Habitat. Lives in water that does not flow very fast, in gravel, sand, or in muddy sand.

Remarks. Alasmidonta heterodon (Lea) is an Atlantic Slope species, not closely related to the other members of the genus. It can be confused with no other unionid in the region because of its distinct dentition. *A. heterodon* has two lateral teeth in the right valve, though the upper one may be rather rudimentary, and one in the left valve. This tooth arrangement is just the opposite of all other Atlantic Slope Unionidae.

This species is usually rare, and its erratic distribution may be merely a reflection of inadequate collecting. Judging from the available records, it appears to be most widely distributed and abundant in the Connecticut River system of Vermont, New Hampshire, Massachusetts, and Connecticut.

Range. Atlantic Slope: Neuse River system, North Carolina, north to the Petitcodiac River system, New Brunswick, Canada, but discontinuous. Known only from the following additional intervening drainage systems; Rappahannock River system, Virginia; Potomac River system, Maryland; Delaware River system, Pennsylvania; Housatonic River system, Connecticut (Linsley, 1845); Quinnipiac River system, Connecticut; Connecticut River system, Vermont, New Hampshire, Massachusetts, Connecticut; Merrimac River system, Massachusetts.

Specimens Examined

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Pooles Bridge [not located]; Neuse River [6 mi. E Raleigh]; Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co. Chicod Creek, Pitt Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Blue Run, Orange Co. (MZUM).

Rappahannock River Drainage. *Virginia:* Mountain Run, Culpeper Co. (Ortmann, 1919: 175).

Potomac River System

Potomac River Drainage. *Maryland*: McIntosh Run, 4 mi. N Leonardtown, St. Marys Co. (H. D. Athearn).

Subgenus *Alasmidonta s.s.* Say

Monodonta Say 1817, Nicholson's Encyclopedia, 2 [no pagination] *non* Lamarck 1799.

Alasmidonta Say 1818, Jour. Acad. Nat. Sci. Phila., ser. 1, 1: 459.

Type species, *Monodonta undulata* Say. Monotypic.

Alasmodonta [*sic*] Say 1819, Nicholson's Encyclopedia, ed. 3, 4 [no pagination].

Hemiodon Swainson 1849, Treatise on Malacology, pp. 288, 381. Species listed: *H. undulatus* [Say], *An. rugosus, purpurascens, areolata* [*all* Swainson], *non Hemiodon* Swainson, *op. cit.*, p. 191.

Type species, *A. undulata* Say. Subsequent designation, Hermannsen, 1847, Indicis Generum Malacozoorum, 1: 527.

Uniopsis Swainson 1840, Treatise on Malacology, pp. 289, 382.

Type species, *U. mytiloides* Swainson and *U. radiata* Swainson. Both names are based on the same fig., no. 64 = *Alasmidonta undulata* (Say).

Bullella Simpson 1900, Proc. United States Natl. Mus., 22: 672.

Type species, *Margaritana arcula* Lea. Original designation.

Jugosus Simpson 1914, Cat. Naiades, 1: 357.

Type species, *Strophitus wrightianus* Walker. Original designation, Simpson, 1900, Proc. United States Natl. Mus., 22: 666. Ortmann, 1914, Nautilus, 28: 45.

Alasmidonta s. s. is restricted to the Apalachicolan and Atlantic Slope regions. There is one other species in this subgenus that is not covered in this paper, *A. wrightiana* (Walker) (Johnson, 1967: 8, pl. 2, fig. 5), from the Ochlockonee River system, Florida.

In addition to the subgenera discussed here, or placed in synonymy above, Frier-

son (1927: 18, 19) includes in his list two other subgenera of *Alasmidonta*, *Pressodonta* Simpson, which appears to be represented in the Interior Basin by a single species, *A. calceola* (Lea); and *Sulcularia* Rafinesque, which Ortmann and Walker (1922: 33) show is not identifiable. The species listed under it belong in the genus *Lasmigona*, subgenus *Alasminota* Ortmann.

Alasmidonta (*Alasmidonta*) *undulata* (Say)
Plate 13: 3–4

Unio undulata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 3 (Delaware and Schuylkill rivers [near Philadelphia, Philadelphia Co., Pennsylvania]; type, not in ANSP [lost]).

Unio glabratus Sowerby 1823, Genera of Recent and Fossil Shells, no. 16, fig. 3 (no locality, type not in British Museum (Nat. Hist.) [lost]). *non* Lamarck 1819.

Alasmidonta sculptilis Say 1829, New Harmony [Indiana] Disseminator, 2, no. 22, p. 339 (Virginia; type not in ANSP [lost]).

Unio hiatus Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, Pt. 2, 2: 235, pl. 54, figs. 2a, b (environs de Philadelphie [Philadelphia Co., Pennsylvania]; type [location unknown]).

Uniopsis radiata Swainson 1840, Treatise on Malacology, p. 289, fig. 62 ([North America] type [location unknown]).

Uniopsis mytiloides Swainson 1840, Treatise on Malacology, p. 382, fig. 62 ([North America] type [location unknown]. [Both this and the preceding were found on the same figure.]

Unio swainsoni Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 76, fig. 396 (Hab. ? figured holotype British Museum [Nat. Hist.] 1900.3.19.21.).

Alasmidonta undulata (Say). Simpson, 1914, Cat. Naiades, 1: 494.

Alasmidonta (*Alasmidonta*) *undulata* (Say) Ortmann 1919, Mem. Carnegie Mus., 8: 117, pl. 11, fig. 7. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 25, fig. 33. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. 183, p. 24, pl. 3, figs. 3, 4.

Description. Shell generally small, from 50 to 65 mm, though sometimes reaching 80 mm in length. Outline elliptical or subrhomboid. Valves somewhat inflated, thin, becoming quite solid anteriorly. Anterior end regularly rounded; posterior end rather broadly pointed. Ventral margin almost always slightly rounded. Dorsal margin short and straight, forming an angle with the obliquely descending posterior margin. Hinge ligament located posteriorly of the umbos, occupying most of the dorsal margin. Posterior ridge rounded, sometimes with a faint second ridge above it. Posterior slope slightly concave, sometimes with irregular oblique corrugations. Umbos rather inflated and somewhat raised above the hinge line, located anterior to the middle of the shell, their sculpture consisting of four or five strong ridges running nearly parallel to the growth lines. These ridges extend some distance on the disk, and posteriorly are angular, thickened, and raised. They are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. Generally the entire surface of the shell is smooth, though occasionally slightly roughened, especially posteriorly; periostracum greenish, yellowish, reddish brown, with more or less distinct green to blackish rays of varying width over the entire surface. The posterior slope is often somewhat lighter than the rest of the shell, with finer and sharper rays. Older shells become blackish, but the rays are still visible through transmitted light.

Left valve with a compressed, sometimes stumpy pseudocardinal tooth, often with a rudimentary one in front; interdentum rather broad, occasionally with a visible but connected interdental tooth; lateral tooth barely distinct. Right valve with one rather high, chunky, subtriangular tooth; often with a broad interdentum; with just a trace of a lateral tooth. Beak cavities moderately deep with muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct anteriorly where the shell is thickened. Nacre white, salmon pink, or reddish, iridescent posteriorly.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
80	51	39	Tar River, Bruce, 9 mi. NW Greenville, Pitt Co., North Carolina.
72	45	31	Neuse River, Falls, Wake Co., North Carolina.
54	32	23	Nottoway River, 3 mi. E Rawlings, Brunswick Co., Virginia.

Anatomy. Discussed by Ortmann (1911: 296). Glochidia are moderately large with strong hooks. They measure 0.34 mm in length and 0.36 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 178) states that this species is clearly bradytictic, with a short interim in June and July.

Habitat. Lives in water that does not flow very fast, in gravel or sand, appears to avoid mud.

Remarks. Alasmidonta undulata (Say), of the Atlantic Slope, is not closely related to any *Alasmidonta* of the Interior Basin. Its nearest relatives are *A. arcula* of the Altamaha River system, Georgia, and *A. triangulata* of the Apalachicolan and Southern Atlantic Slope regions; but both of these species are more triangular in outline, with sharper posterior ridges. *A. undulata* also resembles *A. wrightiana* (Walker) of the Ochlockonee River system, Florida, in shape, and it has a similar tooth structure and rounded posterior ridge, but *wrightiana* has strong ridges which cover the posterior slope, whereas *undulata* is unsculptured.

A. undulata is a common species, especially on the Northern Atlantic Slope, and is often locally abundant. It seems to be somewhat less common on the Southern Atlantic Slope. It avoids the larger rivers, preferring smaller streams, in which it often goes far up toward the headwaters.

Range. Atlantic Slope: Catawba River, North Carolina, of the upper Cooper-Santee River system, north to the lower St. Lawrence River system, Canada.

Specimens Examined

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River (USNM).

Pedee River System

Yadkin River Drainage. *North Carolina:* Uwhairie River (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Morgan Creek, 1 mi. SE Chapel Hill, Orange Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM). Cape Fear River (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Falls (50); Neuse River, 5.75 mi. E Raleigh Center (45); Swift Creek, 3 mi. SSW Garner (20); Middle Creek, 6.25 mi. SE Apex (18); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pinetops, Edgecomb Co. Tar River, Bruce, 9 mi. NW Greenville, Pitt Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407); North [= Maury] River, 2 mi. WNW Lexington (MZUM); North River, Buena Vista (USNM); *all* Rockbridge Co. Rivanna River, 2 mi. W Columbia, Fluvanna Co. James River, opposite Maidens, Goochland Co.

York River System

North Anna River Drainage. *Virginia*: Mine Run, Orange Co. (MZUM).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Blue Run (MZUM); Mountain Run (MZUM); *both* Orange Co.

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington; Marsh Run, Remington (*both* Ortmann, 1919: 180); *both* Fauquier Co.

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.], 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *Maryland*: Wills Creek, Ellerslie, Allegany Co. (Ortmann, 1919: 179). Potomac River, Hancock, Washington Co. (Ortmann, 1919: 179). *Pennsylvania:* Great Tonoloway Creek, Thompson Township, Fulton Co. (Ortmann, 1919: 179). Conococheague Creek, Greencastle and Scotland, Franklin Co. (Ortmann, 1919: 179). *Virginia:* N Fork, Shenandoah River, Broadway, Rockingham Co. (Ortmann, 1919: 179). S River of S Fork, Shenandoah River, Waynesboro, Augusta Co. (Ortmann, 1919: 179). S Fork, Shenandoah River, Elkton, Rockingham Co. Ortmann, 1919: 179). *West Virginia:* Shenandoah River, Harpers Ferry, Jefferson Co. (USNM). *Virginia:* Potomac River, Great Falls, Fairfax Co.

Alasmidonta (Alasmidonta) triangulata (Lea)

Plate 13: 5, 6

Margaritana triangulata Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 138 (Upper Chattahoochee [River], Georgia; Columbus, Georgia; Polato Co. [*sic*] [Potato Creek, Upson Co.], Georgia; Sawney's Creek [about 8 mi. NW Camden, Kershaw Co.], South Carolina). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 228, pl. 32, fig. 111; figured holotype USNM 86249, from Upper Chattahoochee [River], Lea, 1859, Obs. Unio, 7: 46.

Alasmidonta triangulata (Lea). Simpson, 1914, Cat. Naiades, 1: 509. Clench and Turner, 1956, Bull. Florida State Mus., 1: 180, pl. 5, fig. 4.

Strophitus wrightianus Clench and Turner 1956, Bull. Florida State Mus., 1: 180 *non* Walker 1901, Nautilus, 15: 65, pl. 3.

Description. Shell generally small, though reaching 70 mm in length in the Apalachicola River system. Outline subtriangular. Valves inflated, thin to rather solid. Anterior end regularly rounded; posterior end rather broadly pointed. Ventral margin almost always slightly rounded. Dorsal margin short and straight, forming an angle with the obliquely descending posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge high and angular with a second or third faint ridge above it, the second one ending in a slight biangulation near the base of the shell. Umbos full and high, located anterior to the center of the shell, their sculpture consisting of a number of strong ridges running nearly parallel to the growth lines. These ridges extend some distance on the disk and are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. The disk is smooth; the periostracum is usually fine and limited to the posterior slope. Young shells may be yellowish or greenish yellow, often with dark green rays of varying width. Older shells become dark brownish black, but the rays and yellowish ground color are still visible when seen through transmitted light.

Left valve with a compressed, sometimes stumpy pseudocardinal tooth, often with a rudimentary one in front; interdentum broad, occasionally with a visible but connected interdental tooth; lateral tooth barely visible. Right valve with one rather high subtriangular tooth; broad interdentum; lateral tooth barely visible. Beak cavities deep, with dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint.

Pallial line distinct anteriorly where the shell is thickened. Nacre bluish white to salmon pink.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
68	47	38	Savannah River [Johnsons Landing], 10 mi. W Allendale, Allendale Co., South Carolina (MZUM).
48	32	27	Mill Race, 2 mi. N Sardis, Burke Co., Georgia.

Habitat. Prefers sandy mud in rocky pools and eddies of large creeks and rivers.

Remarks. Alasmidonta triangulata (Lea) of the Apalachicolan and Southern Atlantic Slope regions cannot be confused with *A. arcula* (Lea) of the Altamaha River system because it is proportionally not as high. The umbos are anterior to the center, and while incurved, do not render the hinge line concave, and the posterior ridge is not as acutely sharp.

A. triangulata is closest to *A. undulata* (Say) of the Atlantic Slope region, but the latter has a shape which is usually an elongated oval, a very broadly rounded posterior ridge, more ponderous pseudocardinals, and more of an interdentum. In the Apalachicolan region, *A. triangulata* can be confused only with *A. wrightiana* (Walker); the latter has the shape, rounded posterior ridge, and tooth structure of *A. undulata*, differing from *undulata* and *triangulata* in the strong ridges which cover the posterior slope.

A. triangulata is a rare species throughout its range, but is especially so on the Southern Atlantic Slope where each of the lots examined consists of only one or two specimens.

Range. Apalachicolan region: restricted to the Apalachicola River system. Southern Atlantic Slope: Ogeechee and Savannah river systems, Georgia; and Cooper-Santee River system, South Carolina.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Scarboro (MZUM); Ogeechee River, bridge, 1 mi. S Dover; *both* Screven Co. (MZUM).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River [Johnsons Landing], 10 mi. W Allendale, Allendale Co. (MZUM). *Georgia*: Mill Race, 2 mi. N Sardis, Burke Co.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Sawney's Creek [about 8 mi. NW Camden, Kershaw Co.] (USNM).

Alasmidonta (*Alasmidonta*) *arcula* (Lea)

Plate 13: 7, 8

Margaritana arcula Lea 1836, Synopsis Naiades, p. 43 [*nomen nudum*]. Lea, 1838, Trans. Amer. Philos. Soc., 6: 71, pl. 22, fig. 69 (Altamaha [River], Liberty [now Long] Co., Georgia; figured holotype USNM 86170). Lea, 1838, Obs. Unio, 2: 71.

Alasmidonta arcula (Lea). Simpson, 1914, Cat. Naiades, 1: 508.

Description. Shell medium, reaching 75 mm in length. Outline triangular. Valves much inflated, thin but strong. Anterior end regularly rounded; posterior end sharply truncated. Ventral margin straight or slightly rounded. Dorsal margin short and curved, forming a sharp angle with the obliquely truncated posterior margin. Hinge ligament occupying almost all of the posterior dorsal margin. Posterior ridge high and sharply angular, with a second faint ridge above, ending in a slight biangulation near the base of the shell. Posterior slope very truncated. Umbos extremely full and high, located at the center of the shell, their sculpture consisting of a number of strong ridges running nearly parallel to the growth lines. These ridges extend well out on the disk and

posteriorly are angular, considerably thickened, and raised. They are crossed by fine, wrinkled, radiating threads. In front of and behind the regular umbonal sculpture there are radiating lirae. The disk is smooth; the periostracum is usually fine and limited to the posterior slope. Shell dull greenish yellow with distinct green rays of varying length over the entire surface. Mature shells are often blackish, but the rays are still visible through transmitted light.

Left valve with a long compressed pseudocardinal tooth, often with a rudimentary one in front; interdental tooth distinct but connected; lateral teeth barely visible. Right valve with one compressed, triangular tooth; scarcely any interdentum; lateral tooth barely visible. Beak cavities very deep, with dorsal muscle scars under the hinge plate. Anterior adductor muscle scars deep, posterior ones faint. Pallial line distinct anteriorly where the shell is thickened. Nacre bluish white or white.

Sexual differences are not visible in the shell.

Length mm	Height mm	Width mm	
80	60	50	Altamaha River [Long Co.], Georgia.
67	51	44	Ocmulgee River, Hawkinsville, Pulaski Co., Georgia.
50	43	38	Altamaha River, 4 mi. NE Jesup, Wayne Co., Georgia.

Anatomy. Discussed by Lea (1863: 447).

Habitat. Lives in sandy mud below sand bars in sluggish water and eddies.

Remarks. Alasmidonta arcula (Lea) of the Altamaha River system cannot be confused with any other unionid in the Atlantic Slope region, though it is close to *A. triangulata* (Lea), which is found in both the Apalachicolan and Atlantic Slope regions. *Alasmidonta arcula* differs from *triangulata* by being proportionally higher with centrally located umbos which are so elevated as to be incurved, by its concave hinge line, and by its extremely sharp posterior ridge which forms almost a 90° angle with the posterior slope.

This is a rare species; not more than a few specimens have ever been collected at any station in this century save for a series of twenty-two specimens collected by H. D. Athearn in 1962 in the Ocmulgee River, below Lumber City, Telfair Co., Georgia. The old unlocalized specimens of *arcula* in the major museums are presumed to have been collected near the type locality in the tidewater region of the Altamaha River, where it may be, or was, more abundant.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, Hawkinsville; Limestone Creek, near Hartford (H. D. Athearn); *both* Pulaski Co. Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Ohoopee River Drainage. *Georgia*: Ohoopee River, 3 mi. N Leman, Emanuel Co.

Altamaha River Drainage. *Georgia*: Altamaha [River], Liberty [now Long] Co. (USNM). Altamaha River, Fort Barrington, McIntosh Co. (ANSP).

Subgenus *Decurambis* Rafinesque

Decurambis Rafinesque 1831, Continuation of Monograph Bivalve Shells of River Ohio (Phila.), pp. 4, 5. Species listed: *Alasmodon scriptum* Rafinesque and *A. atropurpureum* Rafinesque.

Type species, *Alasmodon scriptum* Rafinesque = *Alasmidonta marginata* (Say). Subsequent designation, Ortmann and Walker, 1922, Occ. Pap. Mus. Zool., Univ. Mich., no. 112, p. 38.

Rugifera Simpson 1900, Proc. United States Natl. Mus., 22: 670.

Type species, *Alasmidonta marginata* Say. Original designation.

The present author follows Ortmann and Walker (1922: 38) and regards *Decuram-*

bis as a subgenus of *Alasmidonta*, though Frierson (1927: 21) raised *Decurambis* to a genus.

Decurambis includes but two allopatric species: *A. marginata* Say (Ortmann, 1919: 181, pl. 12, fig. 3), primarily a species of the Interior Basin, but which is also found on the Northern Atlantic Slope in the Susquehanna and upper St. Lawrence drainage systems; and *A. varicosa* (Lamarck), which is limited in distribution to the Atlantic Slope.

Alasmidonta (Decurambis) varicosa (Lamarck)
Plate 14: 1, 2

Unio varicosa Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 78 (la rivière de Schuglkill [Schuylkill] près de Philadelphie [Philadelphia Co., Pennsylvania]; holotype, Geneva Museum. *teste* Johnson, 1953, Nautilus, 66: 95; aussi dans le lac Champlain, [Vermont]).

Alasmodon corrugata De Kay 1843, Zool. New York, Moll., pt. 5: 198, pl. 24, fig. 259 (Passaic River, New York; type, New York Lyceum of Nat. Hist. [destroyed by fire]).

Mya rugulosa Wood 1856, *in* Hanley, Index Test, p. 199, pl. 1 supp., fig. 7 (North America; type [probably lost]).

Alasmidonta varicosa (Lamarck). Simpson, 1914, Cat. Naiades, 1: 506.

Alasmidonta (Decurambis) varicosa (Lamarck). Ortmann, 1919, Mem. Carnegie Mus., 8: 190, pl. 12, fig. 5. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 28, fig. 34. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. 183, p. 25, pl. 3, figs. 5, 6.

Description. Shell usually small, from 40 to 65 mm, though sometimes reaching 80 mm in length. Outline rhomboid or subelliptical. Valves not much inflated, thin but strong. Anterior end regularly rounded; posterior end slightly elongated and biangulate. Ventral margin straight or slightly arcuate. Dorsal margin straight, forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament located posteriorly of the umbos, short but prominent. Posterior ridge broadly rounded, with a second very faint ridge above it, ending in a biangulation near the base. Posterior slope broadly rounded, with a system of fine radial wrinkles running to the upper posterior margin. Umbos large and somewhat inflated, but not high, located in the anterior third of the shell, their sculpture consisting of three or four thick bars. The disk is smooth; the periostracum is yellowish, greenish, brownish, or blackish, generally with distinct narrow or wide, straight, greenish or blackish rays. The rays are usually broken by growth lines.

Each valve has one thin, distinct, depressed, triangular pseudocardinal; no lateral teeth. Beak cavities moderately deep with muscle scars under the hinge plate; anterior adductor muscle scars deep, posterior ones less so. Pallial line distinct anteriorly where the shell is slightly thickened. Nacre bluish white, often with salmon, pinkish, or purplish shades.

Sexual differences are visible in the shell; females are slightly more swollen in the region of the posterior ridge. Occasionally the swelling is so great that the lateral faces of the shell in front of the ridge appear flat or even concave. The ventral margin may be slightly emarginate, but male shells are also sometimes emarginate so that the sex can not always be ascertained from the shell alone.

Length mm	Height mm	Width mm	
73.0	40.0	31.0	N Fork, Shenandoah River, E Woodstock, Shenandoah Co., Virginia. Female.
44.0	26.0	18.0	Turkey Creek, 8 mi. NW Edgefield, Edgefield Co., South Carolina. Female.
33.0	28.0	12.0	Rocky River, 11 mi. N Sanford, Chatham Co., North Carolina. Male.
32.0	29.5	13.0	As above. Female.

Anatomy. According to Ortmann (1919: 191), the anatomy of this species is very similar to that of *Alasmidonta marginata* Say.

Breeding season. Ortmann (1919: 191) found that in Pennsylvania breeding begins

in August, when eggs are present; glochidia are found in September, and are carried over the winter and discharged the following May.

Habitat. Lives among rocks on gravel substrates; also on sandy shoals, especially in rapids and riffles of small rivers and creeks.

Remarks. Alasmidonta varicosa (Lamarck), having rudimentary pseudocardinals, a lack of lateral teeth, and radial wrinkles on the posterior slope, is distinguishable from the other *Alasmidonta* of the Atlantic Slope region. It is replaced in the upper Tennessee and Cumberland river systems by *A. ravenelina* (Lea) which differs from *varicosa* by being more elongate, by having a more broadly biangulate posterior ridge, and by usually not having more than a trace of radial wrinkles on the posterior slope.

Alasmidonta varicosa is the Atlantic replacement of *A. marginata* Say which is found in the Interior Basin throughout the upper Mississippi drainage, including the Ohio, Tennessee and Cumberland river systems. In the Northern Atlantic Slope region, *marginata* is found in the Susquehanna River, Pennsylvania, and the upper St. Lawrence River, Canada. *A. marginata* has a very sharp posterior ridge and a truncated posterior slope, which renders the shell subtrapezoidal; also, the rays tend to be broken into spots. *A. varicosa* has a gradually rounded, broadly biangulate posterior ridge, a gently rounded posterior slope, and a rhomboidal shape. The rays are never broken into spots; the shell is not as heavy, nor does it grow as large as does *marginata*. Though *marginata* prefers larger rivers while *varicosa* prefers smaller streams, they are nevertheless sometimes found together where their ranges overlap, but they are easily separated.

Simpson (1914, 1: 506) correctly recorded this species from as far south as South Carolina, but I was unable to find the material on which his record was based. Ortmann (1919: 193) personally collected *A. varicosa* in the upper Catawba River, North Carolina, and Clench and Okkelberg collected a single specimen in 1929 in a tributary of the Savannah River, South Carolina. Seemingly rare below the Potomac River, Maryland, *A. varicosa* is relatively abundant on the Northern Atlantic Slope.

Range. Atlantic Slope: tributary of the upper Savannah River system, South Carolina, north to the lower St. Lawrence River system, Canada.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Turkey Creek, 8 mi. NW Edgefield, Edgefield Co. (MZUM).

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Bridgewater, Burke Co. (Ortmann, 1919: 193).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co.

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407 as *A. marginata* Say).

Occoquan Creek System

Occoquan Creek Drainage. *Virginia*: Broad Run [Fairfax Co.], 3 mi. W Manassas, Prince William Co.

Potomac River System

Potomac River Drainage. *Virginia*: N Fork, Shenandoah River, E Woodstock, Shenandoah Co. S Fork, Shenandoah River, Riverton, Warren Co. *Maryland:* Potomac River, Hancock, Washington Co. (Ortmann, 1919: 193).

Genus *Anodonta* Lamarck
Subgenus *Anodonta s.s.* Lamarck

Anodonta Lamarck 1799, Mémoires de la Soc. d'Hist. Nat. de Paris, p. 87.

Type species, *Mytilus cygneus* Linnaeus. Monotypic. Placed on the Official List of Generic Names in Zoology, in 1926, Opinion 94. Reconfirmed, 1959, Opinions and Declarations rendered by Int. Comm. Zool. Nomen., 20 (28): 303–10, Opinion 561.

Ortmann, 1912, Ann. Carnegie Mus., 8: 286, *partim*. *Anodonta s. s.* is found primarily in the Palearctic region of Europe and Asia and like the type species may be monoecious and have flat umbones. The several western American species of the Pacific region clearly belong to *Anodonta s. s.*

Subgenus *Pyganodon* Crosse and Fischer

Pyganodon Crosse and Fischer 1894, *in* Fischer and Crosse, Mission Sci. au Mexique, pt. 7, 2: 518. Species listed: *A. globosa* Lea; *A. tabascens* Morelet; *A. nopalatensis* Sowerby; *A. grijalvae* Morelet; *A. glauca* Valenciennes. Introduced as a section.

Type species, *Anodonta globosa* Lea. Subsequent designation, Frierson, 1927, Check List North American Naiades, p. 9, *teste* Errata et Corrigenda. Raised to a subgenus.

Frierson (1927: 14–16) used *Pyganodon* as a subgenus to include most of the *Anodonta* of middle and eastern North America.

It is suspected that when the Interior Basin taxa included in this subgenus are revised, it will be found that there are about an equal number of species in the Interior Basin and Atlantic Slope region.

Anodonta (Pyganodon) cataracta cataracta Say
Plate 14: 3, 4
Plate 15: 1

Anodonta fluviatilis Gmelin, of authors. See note under *Lampsilis ochracea* Say, p. 388.

Anodonta cataracta Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 2 (deep part of a mill dam [presumably near Philadelphia, Philadelphia Co., Pennsylvania, and here so restricted]; type, ANSP [lost]). Simpson, 1914, Cat. Naiades, 1: 386. Ortmann, 1919, Mem. Carnegie Mus., 8: 152, pl. 10, fig. 5, pl. 11, fig. 1. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 39, fig. 46. Athearn and Clarke, 1962, Natl. Mus. Canada Bull. no. 183, p. 27, pl. 2, figs. 5, 6.

Anodonta marginata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 5 (very common in our rivers [presumably near Philadelphia, Philadelphia Co., Pennsylvania, and here so restricted]; type, ANSP [lost]). Simpson, 1914, Cat. Naiades, 1: 388 [*partim*]. The measurements in the description, as transcribed into millimeters, indicate the type to have been 51 mm in length and 38 mm in height. The figured shell was 69 mm in length and 36 mm in height. The first set of dimensions are those of a *cataracta* from a creek environment, while the second are of the elongated form which is sometimes found in ponds, and which becomes more common in the northern range of *cataracta*.

Anodonta teres Conrad 1834, New Fresh Water Shells United States, p. 47, pl. 7, fig. 2 (Santee Canal [Berkeley Co.], South Carolina [type, ANSP lost]). Simpson, 1914, Cat. Naiades, 1: 390.

Anodon excurvata De Kay 1843, Zool. of New York, Moll., pt. 5, p. 202, pl. 17, fig. 233 (Shaker Pond, Niskayuna, Albany Co., New York; Passaic River [Paterson, Passaic Co., New Jersey]; type, New York State Colln., now in USNM [not yet located]).

Anodonta virgulata Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 86 (Roanoke River, Weldon [Halifax Co.], North Carolina; Washington Co., Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 213, pl. 33, fig. 282; figured holotype USNM 86593 from Roanoke River. Lea, 1863, Obs. Unio, 9: 35.

Anodonta lacustris Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 84 (Crooked Lake and Little Lakes [Herkimer Co.], New York). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 363, pl. 62, fig. 188; figured type USNM [not located]; though a slightly smaller specimen, USNM 86597 marked Mohawk, New York, ex Lewis, is labeled holotype. Lea, 1860, Obs. Unio, 8: 45.

Anodonta hallenbeckii Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 138 (Uphaupee [Uphapee] Creek, Macon Co., Georgia [Alabama]). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 50, pl. 32, fig. 112; figured holotype USNM 86428. Lea, 1859, Obs. Unio, 7: 50. Simpson, 1914, Cat. Naiades, 1: 392. Clench and Turner, 1956, Bull. Florida State Mus., 1: 186, pl. 9, fig. 1.

Anodonta gesneri Lea, 1858, Proc. Acad. Nat. Sci. Phila., 10: 139 (Uphaupee [Uphapee] Creek, Macon Co., Georgia [Alabama]). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4:

231, pl. 31, fig. 109; figured holotype USNM 86427. Lea, 1859, Obs. Unio, 7: 49.

Anodonta dariensis Lea 1858, Proc. Acad. Nat. Sci. Phila., 10: 139 (Hopeton, near Darien [McIntosh Co.]; Swift Creek, near Macon [Bibb Co.]; Flint River; *all* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 230, pl. 28, fig. 99; figured holotype USNM 86600 from Swift Creek. Lea, 1859, Obs. Unio, 7: 48. Simpson, 1914, Cat. Naiades, 1: 394.

Anodonta williamsii Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Potomac River at the White House [District of Columbia]; below Mount Vernon [Fairfax Co., Virginia]; Othcalooga Creek [Gordon Co.], Georgia. Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 27, pl. 10, fig. 26; type, USNM [not located]. Lea, 1867, Obs. Unio, 11: 31.

Anodonta tryoni Lea 1862, Proc. Acad. Nat. Sci. Phila., 14: 169 (Schuylkill River above Philadelphia; Delaware River at League Island [*both* Philadelphia Co., Pennsylvania]; Flemington [= Farmington, Hartford Co.], Connecticut; Westfield [Hampden Co.], Massachusetts; Potomac River near Chain Bridge, above Washington, D. C.). Lea, 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 28, pl. 10, fig. 27; type, USNM [not located], paratype, USNM 86572 from Potomac River. Lea, 1867, Obs. Unio, 11: 32.

Anodonta dolearis Lea 1863, Proc. Acad. Nat. Sci. Phila., 15: 193 (Stewart's Mill Dam, Union Co., North Carolina). Changed to:

Anodonta doliaris Lea 1866, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 24, pl. 8, fig. 23; figured holotype ANSP 126522a. Lea, 1867, Obs. Unio, 11: 28. Simpson, 1914, Cat. Naiades, 1: 393.

Description. Shell medium to large, reaching over 165 mm in length. Outline subelliptical, more or less elongate. Valves of young specimens not much inflated, those of older ones quite inflated, thin, sometimes very thin. Anterior end regularly rounded; posterior end rather pointed. Ventral margin straight, or slightly curved, very occasionally slightly incurved. Dorsal margin slightly curved, often forming a winglike angle where it meets the obliquely descending posterior margin. The posterior margin joins the ventral margin in a broad point, somewhat below the medial line. Hinge ligament long and low. Posterior ridge indistinct. Posterior slope slightly concave, sometimes with two faint ridges. Umbos slightly swollen and moderately convex, located in the anterior third or fourth of the shell, their sculpture consisting of five to seven double-looped bars, not appreciably lower in front or behind the sinus, but of uniform elevation. Periostracum generally smooth and shiny, slightly roughened toward the margins and on the posterior slope. Surface of the shell sometimes uniformly straw yellow, but usually lighter to darker green with concentric lighter and darker bands, with darker rays on the disk. The rays on the posterior slope are darker, at least those rays on the faint ridges, though generally the whole posterior slope is blackish green.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent.

Females are sometimes indicated by a swelling of the valves posterior to the middle, but this is not a uniform character.

Length mm	Height mm	Width mm	
165	86	62	Lake Michie, 12 mi. NNE Durham, Durham Co., North Carolina.
152	79	65	Savannah River, Johnsons Landing, 10 mi. W Allendale, Allendale Co., South Carolina (MZUM).
107	58	49	Swift Creek, near Macon [Bibb Co.], Georgia. Holotype of *A. dariensis* Lea.

Anatomy. Thoroughly discussed by Simpson (G. B., 1884) and commented upon by Reardon (1929: 8, pl. 3, figs. 1–10). The glochidia are hooked.

Breeding season. From August to May (Ortmann, 1919: 154).

Habitat. Lives in rivers and creeks in soft mud and sand; also in sand bars, generally in slowly moving water; prefers ponds.

Remarks. In the Atlantic Slope region *Anodonta cataracta* Say can be confused in the lower St. Lawrence drainage with *Anodonta cataracta fragilis* Lamarck (see Athearn and Clarke, 1962: 28; 1963: 22); *Anodonta implicata* Say under which see:

Remarks on p. 361; and in central New York with *Anodonta grandis* Say, of the Interior Basin. *A. cataracta* Say differs from *grandis* primarily in the umbonal sculpture, that of the latter consists of four to five bars of which the first two are concentric, while the others are distinctly double-looped, with a sharp re-entering sinus between the loops. The anterior loop is broadly rounded, the posterior loop is angular, narrow, and characteristically elevated into a tubercle. In *cataracta* the bars are of uniform height and are not tubercular. These distinctions were properly pointed out by Marshall (1890: 188, 189). Except for this minor difference the two species are very close, though *cataracta* tends to be a brighter green, and while short high examples of *cataracta* are found in rivers, these forms are more common in *grandis*. In general, *cataracta* is more elongated, especially individuals from ponds, and the posterior point is more elevated above the base line, rendering the ventral margin more convex. Ortmann (1919: 154) has clearly pointed out the different reaction of the two species to environment.

Specimens from the Alabama-Coosa River system show no morphological differences separating *hallenbeckii* (Lea) (Clench and Turner, 1956: 186) from *cataracta*. It is possible that *cataracta* arrived there through the commingling of the upper Alabama and Coosa rivers directly, though it is suggested elsewhere in this paper that *cataracta* may more likely have spread into the Apalachicola River system through a confluence of it with the Savannah, and then subsequently reached the Alabama system through a mingling of the waters of its Uphapee Creek and Uchee Creek of the Apalachicola River system. Most of the shells from Uphapee Creek are the long pond forms. I did not find any *Anodonta* in this broad, swift flowing creek in 1964, suggesting that the original lot was from a quiet backwater which I did not locate.

In the southern part of the Atlantic Slope *A. cataracta* is not very common. In the Altamaha River, at the stations listed below, only a few specimens were taken. Lea's specimen of *dariensis* from Hopeton, near Darien, McIntosh Co., Georgia, was not located, hence it is not included in the records since it might be *gibbosa*. In the Museum of Comparative Zoology there is a single specimen of *cataracta* from the C. B. Adams collection made before 1850, labeled Washington Co., Georgia. If this record is valid, then *cataracta* is found either in the upper Oconee River of the Altamaha River system or in the upper Ogeechee River system. This species becomes abundant and reaches large size in impounded waters, such as Lake Moultrie of the Cooper-Santee River system, South Carolina, Stewarts Mill Dam, Union Co., North Carolina, and Lake Michie on Flat River, North Carolina.

Range. Alabama-Coosa River system. Apalachicolan region: Choctawhatchee and upper Apalachicola River systems. Atlantic Slope: Altamaha River system, Georgia, north to the lower St. Lawrence River system, Canada. Interior Basin: probably extending from the St. Lawrence River system westward to Michigan.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Possum Lake, NE Stone Mountain, De Kalb Co. Swift Creek, near Macon, Bibb Co. Limestone Creek, near Hartford, Pulaski Co. (H. D. Athearn). Dicksons Creek, 10 mi. NE Fitzgerald, Ben Hill Co. Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River, 6 mi. S Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* (MZUM); *both* Allendale Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Catawba River Drainage. *North Carolina*: Bissels Pond, Charlotte, Mecklenburg Co. (USNM).

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Poplar Creek, Schulers Fish Pond, near Santee State Park; Eutaw Springs, [town of] Eutaw Springs; *both* Orangeburg Co. Lake Moultrie, Cross, Berkeley Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (USNM). Yadkin River, Rowan Co. Stewarts Mill Dam, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Travis Creek, 1.5 mi. N Gibsonville, Guilford Co. (MZUM). Rocky River, 11 mi. N Sanford, Chatham Co. Livingstons Creek [Brunswick Co.] (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Lake Michie, 12 mi. NNE Durham Center, Durham Co. (75).

Roanoke River System

Dan River Drainage. *Virginia*: Aarons Creek, 3 mi. W Buffalo, Lithia Springs; Dan River; *both* Halifax Co.

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co. (USNM).

James River System

James River Drainage. *Virginia*: Calfpasture River (Conrad, 1846: 407).

Rappahannock River System

Rapidan River Drainage. *Virginia*: Mountain Run, Orange Co. (MZUM).

Potomac River System

Potomac River Drainage. *Pennsylvania:* Great Tonoloway Creek, Thompson Township, Fulton Co. (Ortmann, 1919: 156). Conococheague Creek, Greencastle, Franklin Co. (Ortmann, 1919: 156). *West Virginia:* South Branch, Potomac River, Romney, Hampshire Co. (Ortmann, 1919: 157). *Virginia:* South River (upper Shenandoah River), Waynesboro, Augusta Co. (Ortmann, 1919: 157). Potomac River, Great Falls Co. Park, Fairfax Co. *District of Columbia:* Aqueduct Lake.

Anodonta (Pyganodon) gibbosa Say
Plate 15: 2, 3

Anodonta gibbosa Say 1824 *in* W. H. Keating, Narrative of an Expedition to the Source of the St. Peters River, 2: 265, pl. 14, figs. 3–4 (South Carolina; type, ANSP [lost]. Type locality is here restricted to Altamaha River, Hopeton, near Darien, McIntosh Co., Georgia. See: *Remarks* below). Simpson, 1914, Cat. Naiades, 1: 397.

Anodonta gibbosa Say, *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: 184.

Description. Shell medium to large, reaching 120 mm in length. Outline subelliptical. Valves very much inflated, thin and smooth. Anterior end regularly rounded; posterior end broadly rounded or somewhat pointed. Ventral margin usually broadly curved, though centrally sometimes straight, or slightly incurved. Dorsal margin slightly curved, usually forming a distinct winglike angle where it meets the obliquely descending posterior margin. The posterior margin joins the ventral margin in a broad point near the medial line. Hinge ligament long and low. Posterior ridge broadly rounded, though occasionally with a trace of an angle. Posterior slope slightly concave. Umbos very high and broad, located in the anterior third of the shell, their sculpture consisting of a number of low double-looped ridges. Perios-

tracum generally smooth and shiny, slightly roughened toward the margins and on the posterior slope. Surface of the shell straw yellow to greenish, older specimens becoming chestnut to blackish. Usually with very fine greenish rays; the several on the posterior slope usually darker and broader than those on the disk.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent, sometimes pinkish toward the umbonal cavities.

Length mm	Height mm	Width mm	
123	72	69	Altamaha River, 3 mi. NW Everett City, Glynn Co., Georgia.
97	59	48	Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville, Pulaski Co., Georgia.
74	49	40	[after Say].
71	47	37	Altamaha River, Hopeton, near Darien, McIntosh Co., Georgia.

Habitat. Lives in soft mud and sand, also in sand bars; generally in slowly moving water.

Remarks. In the Atlantic Slope region, *Anodonta gibbosa* Say can only be confused with *A. cataracta* Say, but *gibbosa* has a very swollen shell, the umbos are greatly protruded, and the swelling continues with the growth of the shell, the greatest swelling extending toward the posterior ventral margin. Frierson (1912: 129) correctly pointed out the relationship of this species to *A. cataracta* Say based on the beak sculpture, but thought *gibbosa* might be merely a subspecies. They appear to be separate and both species occur in the Altamaha River system.

It is obvious that Major Le Conte who sent T. Say the type of *gibbosa* made a mistake as to its locality, since there are no specimens of this species in any of the collections studied from South Carolina. Le Conte was to later send I. Lea numerous species he collected in the lower Altamaha River, so it is presumed that this species was also from this region, especially since a specimen in the Museum of Comparative Zoology from B. Walker, collected at Hopeton on the lower Altamaha, has almost the same measurements as the type. To avoid confusion the restriction of the type locality to this region seems warranted.

Clench and Turner (1956: 185) included under this name the *Anodonta* of the Ochlockonee, Apalachicola and Choctawhatchee River systems, but these *Anodonta* are more elliptical and elongate, much less globose, and with the more tuberculous beak sculpture of *Anodonta grandis* Say, which they appear to be.

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Cedar Creek, Fountains Mill, 7 mi. SW Hawkinsville, Pulaski Co. Ocmulgee River, 1 mi. S Lumber City, Telfair Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Buttonwood Swamp, Liberty [now Long] Co. Altamaha River, Hopeton, near Darien, McIntosh Co.

Anodonta (*Pyganodon*) *implicata* Say

Plate 15: 4
Plate 16: 1, 2

Anodonta implicata Say 1829, New Harmony [Indiana] Disseminator 2, no. 22, p. 340 (pond in Danvers [Essex Co.], Massachusetts; type, ANSP [lost]).

The type locality was changed to Agawam River (outlet of Halfway Pond), Plymouth [Plymouth Co.], Massachusetts, and a neotype MCZ 176769 was selected by Johnson, 1946, Occ. Papers on Moll., 1: 112, pl. 16, figs. 1, 2). Simpson, 1914, Cat. Naiades, 1: 391. Ortmann, 1919, Mem. Carnegie Mus., 8: 159, pl. 11, figs. 2, 3. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 40, fig. 42. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 26, pl. 2, figs. 1, 2.

Anodonta newtonensis Lea 1838, Trans. Amer. Philos. Soc., 6: 79, pl. 21, fig. 66 (Newtown [Newton] Creek, [Camden Co., New Jersey], opposite Philadelphia; figured type not in USNM or ANSP [lost]; Schuylkill [River], Fairmount [Philadelphia, Philadelphia Co., Pennsylvania], lectotype USNM 86561 selected by Johnson, 1946, Occ. Papers on Moll., 1: 112. [The selection of lectotypes, without figuring them, is a dubious contribution to knowledge, if, indeed, such selections are valid at all.] Figured here, Pl. 15: 4. Lea, 1838, Obs. Unio, 2: 79.

Anodonta housatonica Linsley 1845, Amer. Jour. Sci., ser. 1, 48: 277 (Housatonic [River], Corum [near Huntington, Fairfield Co.], Connecticut), [*nomen nudum*]. Gould, 1848, Amer. Jour. Sci., ser. 2, 6: 234, figs. 4, 5; measured and figured holotype USNM 678302.

Description. Shell medium to large, reaching 165 mm in length. Outline elongate-elliptical to elongate-ovate. Valves quite inflated, somewhat subcylindrical, rather solid and heavy for an *Anodonta*. Anterior end regularly rounded; posterior end more acutely rounded, older specimens often becoming subtruncated. Ventral margin slightly rounded, becoming straight or slightly arcuate in old individuals. Dorsal margin straight, occasionally forming a slight winglike angle where it meets the obliquely descending posterior margin. Hinge ligament long and low. Posterior ridge not very acute, but generally distinctly biangulate. Posterior slope slightly concave. Umbos slightly swollen and moderately convex, located in the anterior third of the shell, their sculpture consisting of five to seven double-looped bars, not appreciably lower in front or behind the sinus but of uniform elevation. Periostracum generally rather smooth, save for growth lines and occasional plaiting, yellowish brown or greenish brown, sometimes becoming reddish brown or almost black in old specimens. Immatures are sometimes greenish and obscurely rayed.

No hinge plate or teeth. Beak cavities rather shallow. Muscle scars and pallial line distinct especially in mature specimens. Shell distinctly thickened along the anterior margin below the pallial line. Nacre dull opalescent, generally pale copper, pinkish, or, more rarely, white or bluish white, sometimes with a bluish cast toward the margins.

Females are usually more swollen than males in the middle portion of the disk, which tends to make the lower margin more curved and the shell somewhat shorter and higher than that of the male, but this is not a uniform character.

Length mm	Height mm	Width mm	
162	77	66	Agawam River, Plymouth, Plymouth Co., Massachusetts. Male.
120	60	48	As above. Neotype of *A. implicata* Say. Male.
97	52	39	Schuylkill River, Fairmount, Philadelphia Co., Pennsylvania. Lectotype of *A. newtonensis* Lea. Female.
94	51	34	Housatonic River, Corum, Fairfield Co., Connecticut. Holotype of *A. housatonica* Gould. Male.

Anatomy. The anatomy of this species has not been investigated. The glochidia are rather large, subtriangular, with a spine at the tip of each valve. The host fish is the alewife, *Alosa pseudoharengus* (Wilson) (Johnson, 1946: 112).

Breeding season. According to Ortmann (1911: 303) all *Anodonta* are bradytictic, or winter breeders, the marsupia filling sometime in summer between July and September. The glochidia are carried through the winter and set free when warmer weather begins. I collected gravid females at Plymouth, Massachusetts, on May 8, 1943, and June 9, 1946.

Habitat. Lives in sand or gravel, rarely in mud. Found abundantly, close to the coast in ponds that have an unobstructed outlet to the ocean. Seems to prefer a stream environment; the largest examples have been taken in a relatively swift, sandy stream.

Remarks. Anodonta implicata Say of the

Northern Atlantic Slope can generally be easily separated from all other species of *Anodonta*. The most reliable and constant feature in identifying adults of this species is the pronounced thickening of the anterior-ventral portion of the shell below the pallial line. This thickening is not always pronounced in immatures, but may still be detected. Other characteristics of this species are the dark and usually yellowish or brownish rayless periostracum and the pale copper or salmon color of the nacre.

Anodonta implicata is especially abundant in the region of Cape Cod, Massachusetts, where it reaches its greatest size. The tide waters of the Potomac River, Virginia, seem to be its southern terminus. All the specimens under this name I have seen from rivers below the Potomac were heavy *cataracta*, which have an especially distinct pallial line anteriorly, but which lack the special anterior-ventral thickening of the shell and the characteristic nacre color. It is on the basis of such specimens that Athearn and Clarke (1962: 26) suggest that this species extends to South Carolina.

Range. Northern Atlantic Slope: Potomac River, Maryland, north to New Brunswick and northern Nova Scotia, *both* Canada.

Specimens Examined

Potomac River System

Potomac River Drainage. *District of Columbia:* Potomac River (USNM).

Subgenus *Utterbackia* F. C. Baker

Utterbackia F. C. Baker 1927, American Midland Nat., 10: 221, 222 (misspelled as *Utterbachia* on p. 221).

Type species, *Anodonta imbecillis* [*sic*] Say. Original designation.

Utterbackiana Frierson 1927, Check List North American Naiades, p. 17.

Type species, *Anodonta suborbiculata* Say. Monotypic.

Under the subgenus *Lastena* Rafinesque (not available for use here since the type is *Anodonta lata* Rafinesque, *teste* Ortmann and Walker, 1922: 32), Frierson included all of the taxa mentioned in the present paper, except *A. suborbiculata* Say of the Interior Basin for which he introduced the subgeneric name *Utterbackiana*, on the basis that that species is dioecious. But, as mentioned below, this as an unreliable basis for classification and the shell morphology is clearly that of *Utterbackia*.

Morrison (*in* Walter, 1956: 265) states that *Anodonta imbecilis*, like *A. cygnea* of Europe and Asia, is monoecious and has flat umbos, and that therefore *imbecilis* belongs to *Anodonta s. s.*

Heard (1966: 31) has clearly shown that sexuality is an unreliable means of classifying *Anodonta*. Neither *cygnaea* nor *imbecilis* are uniformly monoecious. The flat umbos of *Utterbackia* and *Anodonta s. s.* appear to be a convergent character. *Utterbackia* is quite isolated from *Anodonta s. s.* in North America, the latter being restricted to the Pacific region. All four species of *Utterbackia* are more delicate than *cygnea*, and some individuals of each of the species exhibit fine rays toward the umbos. These are lacking in *cygnea* or any other *Anodonta*.

There are two species of *Utterbackia* in the Interior Basin, *suborbiculata* and *imbecilis*. The latter is found almost everywhere to the east except Peninsular Florida and the Northern Atlantic Slope region. Speciation has taken place in the Southeastern states, where two species, in addition to *imbecilis*, occur. They are *couperiana* Lea, covered here, and *A. peggyae* Johnson (1965), which occurs in the Apalachicolan region and Gulf drainage of Peninsular Florida.

Anodonta (*Utterbackia*) *imbecilis* Say
Plate 16: 3

Anodonta (*Lastena*) *ohiensis* Rafinesque 1820, Ann. Gén. Sci. Physiques (Bruxelles), 5: 316 (l'Ohio et toutes les rivières adjacentes; supposed type, ANSP 216908, is *Proptera laevissima* (Lea)). Ortmann and Walker (1922, Occ. Papers, Mus. Zool. Univ. Michigan, no. 112, p.

37) clearly showed that *A. ohiensis* is not identifiable, nevertheless Frierson (1927, Check List North American Naiades, p. 18) persisted in using this name for *A. imbecilis* Say.

Anodonta imbecilis Say 1829, New Harmony [Indiana] Disseminator, 2(23): 355. (Wabash River, Indiana; type, ANSP [lost]). Neotype Senckenberg Mus. 4301 [not seen] selected, but not figured, by Haas, 1930, Senckenbergiana, 12: 326. Type locality restricted to Wabash River, New Harmony, Indiana, by Clench and Turner, 1956, Bull. Florida State Mus., 1: 188.

Anodonta incerta Lea 1834, Trans. Amer. Philos. Soc., 5: 56, pl. 6, fig. 16 (Ohio River, near Cincinnati [Hamilton Co., Ohio]; type, not in USNM or ANSP [lost]. Lea, 1834, Obs. Unio, 1: 158.

Anodon horda Gould 1855, Proc. Boston Soc. Nat. Hist., 5: 229 (Comanche Creek [Tributary of The Llano River, close to the present site of Mason, Mason Co.], Texas [*teste*, Taylor, 1967, Veliger, 10: 153]; measured holotype USNM 678301).

Anodonta henryana Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 102 (Matamoras, Tamaulipas [State], Mexico). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 373, pl. 66, fig. 198; figured holotype USNM 86692. Lea, 1860, Obs. Unio, 8: 55.

Utterbackia imbecillis [*sic*] *fusca* Baker 1927, American Midland Nat., 10: 222 (Sturgeon Bay, Door Co., Wisconsin; holotype MZUM 209141, figured by Baker, 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2): 175, pl. 103, fig. 14).

Anodonta imbecillis [*sic*] Say. Simpson, 1914, Cat. Naiades, 1: 396.

Anodonta henryana Lea. Simpson, 1914, Cat. Naiades, 1: 396.

Anodonta ohiensis Rafinesque. Ortmann, 1919, Mem. Carnegie Mus., 8: 162.

Anodonta imbecilis Say, *partim*. Clench and Turner, 1956, Bull. Florida State Mus., 1: p. 187. See: Johnson, 1965, Breviora, Mus. Comp. Zool., no. 213, pl. 2, fig. 5, 6.

Anodonta (*Utterbackia*) *imbecilis* Say. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 40, fig. 42.

Description. Shell small to medium, usually not reaching over 90 mm in length. Outline rather elongated, subelliptical. Valves compressed, or only slightly swollen in young shells, but often becoming quite inflated with age, very thin, fragile, and smooth. Anterior end regularly rounded; posterior end somewhat pointed. Ventral margin slightly convex, often almost straight in the middle. Dorsal margin straight and long, usually forming a distinct angle where it meets the obliquely descending posterior margin. The posterior margin joins the curved ventral margin in a point near the medial line. Hinge ligament short and inconspicuous. Posterior ridge broadly rounded, though occasionally rather angular. Posterior slope slightly concave. Umbos low and broad, seldom extending above the dorsal margin, located in the anterior third of the shell, their sculpture consisting of a number of delicate subconcentric undulations. Periostracum smooth and shiny, except the posterior slope which may be slightly roughened. Surface of the shell straw yellow to greenish yellow, but more generally darker green, sometimes grass green. Toward the umbos the color may be greyish, brownish or yellowish, with concentric darker growth-rests. The disk may be obscurely rayed; the posterior slope usually has two or three dark green to blackish rays.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent, sometimes pinkish toward the umbonal cavities.

This species is hermaphroditic and does not show any sexual differences.

Length mm	Height mm	Width mm	
90	42	34	Magnolia Springs, Magnolia State Park, Perkins, Jenkins Co., Georgia.
84	44	31	Outlet of Waynesboro Lake, Waynesboro, Burke Co., Georgia.
71	39	24	Buck Creek, 5 mi. NW Hawkinsville, Pulaski Co., Georgia.

Anatomy. Clarke (1959: 42) discusses the work that has been done on the anatomy of this species. He suggests that the host fish is *Semotilus atromaculatus atromaculatus* (Mitchill).

Breeding season. Ortmann (1919: 163) says this species is undoubtedly brady-tictic.

Habitat. Lives in soft mud or sand in ponds, creeks, and near the banks of larger rivers.

Remarks. In the Atlantic Slope region, *Anodonta imbecilis* Say can only be confused with *A. couperiana* Lea and in the Apalachicolan region it can only be mistaken for *Anodonta peggyae* Johnson. These three species of *Anodonta* are the only ones in these drainage systems whose umbos do not extend above the dorsal margin. In *imbecilis* the ventral margin is almost parallel to the dorsal one, while in *couperiana* the ventral margin is broadly curved, which renders the shell much higher in proportion to its length than *imbecilis*. See: *Remarks* under *Anodonta couperiana* Lea on p. 365.

The general distribution of *A. imbecilis* has been discussed by Ortmann (1919: 165). It is found in the Apalachicolan region east to the Ochlockonee River system, Florida. In the Atlantic Slope region it does not extend below the Altamaha River system, Georgia. It apparently does not occur in Peninsular Florida, since the author made an extensive collecting trip to this area in 1962 and did not find *A. imbecilis*. It is replaced on the Gulf side of Florida by *Anodonta peggyae* Johnson (1965: 1) and by *A. couperiana* Lea on the Atlantic side. (See: Johnson, 1965, pl. 1.) On the Atlantic slope, *A. imbecilis* extends to the Nottoway River, Virginia, of the Chowan River system. Ortmann (1919: 163) records this species from Pennsylvania in the region of Lake Erie, but not from the Atlantic Slope. It has since been found at Gunpowder River, Loch Raven Dam, Loch Raven, Baltimore Co., Maryland (ANSP).

Range. Interior Basin: Mississippi drainage generally, Ohio River, West Gulf Coastal region, Alabama-Coosa River system; and Apalachicolan region: Rio Grande River system, Texas, east to the Ochlockonee River system, Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Chowan River system. Northern Atlantic Slope: Gunpowder River system, Maryland.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Buck Creek, 5 mi. NW Hawkinsville; Cedar Creek, Fountains Mill, 7 mi. WSW Hawkinsville; *both* Pulaski Co.

Ohoopee River Drainage. *Georgia*: Yam Grande Creek, 3 mi. W Swainsboro, Emanuel Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 4 mi. NE Jesup, Wayne Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Magnolia Springs, Perkins, Jenkins Co. Mill Creek, 5 mi. E Midville; Barkcamp Creek, 7 mi. E Midville; *both* Burke Co.

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, 7.5 mi. NE Shellbluff; outlet of Waynesboro Lake, Waynesboro; Savannah River, 6 mi. NE Girard; *all* Burke Co. *South Carolina:* Savannah River, 6 mi. S Martin; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *all* Allendale Co.

Cooper-Santee River System

Catawba River Drainage. *North Carolina*: Bissels Pond, Charlotte, Mecklenburg Co. (ANSP; USNM).

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina*: Santee River, above dam, near Cross; Charleston (USNM); *both* Berkeley Co.

Pedee River System

Yadkin River Drainage. *North Carolina:* Salem, Forsyth Co. (USNM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Mill Pond, Wilmington, New Hanover Co. (Ortmann, 1919: 164).

Chowan River System

Nottoway River Drainage. *Virginia*: Birchen Lake, on Birchen Creek, Camp Pickett, Nottoway Co.

Gunpowder River System

Gunpowder River Drainage. *Maryland*: Gunpowder River, Loch Raven Dam, Loch Raven, Baltimore Co. (ANSP).

Anodonta (Utterbackia) couperiana Lea
Plate 16: 4
Plate 17: 1

Anodonta cowperiana [*sic*] Lea 1840, Proc. Amer. Philos. Soc., 1: 289 (Hopeton, near Darien [McIntosh Co.], Georgia). Changed to:

Anodonta couperiana Lea 1842, Trans. Amer. Philos. Soc., 8: 227, pl. 20, fig. 46; figured type, not in USNM [lost]. Lectotype, USNM 86673, selected by Johnson, 1965, Breviora, Mus. Comp. Zool., no. 213, p. 3, pl. 2, fig. 4. Lea, 1842, Obs. Unio, 3: 65.

Anodonta dunlapiana Lea 1842, Proc. Amer. Philos. Soc., 2: 225 (South Carolina). Lea, 1842, Trans. Amer. Philos. Soc., 8: 248, pl. 27, fig. 65; figured type, not in USNM [lost]. Lectotype, here selected, USNM 86564, Pl. 17, fig. 1, [Charleston, Chatham Co.] South Carolina. Lea, 1842, Obs. Unio, 3: 86.

Anodonta cowperiana [*sic*] Lea. Clench and Turner, 1956, Bull. Florida State Mus., 1: 183, pl. 6, fig. 3.

Description. Shell medium to large, reaching 110 mm in length. Outline subelliptical to subcircular. Valves somewhat inflated, thin, fragile, and smooth. Anterior end regularly rounded; posterior end somewhat pointed. Ventral margin broadly curved. Dorsal margin straight and long, usually forming a distinct winglike angle where it meets the obliquely descending posterior margin. Hinge ligament short but prominent. The posterior margin joins the curved ventral margin in a point near the medial line. Posterior ridge broadly rounded. Posterior slope slightly concave. Umbos low and broad, seldom extending above the dorsal margin, located in the anterior third of the shell, their sculpture consisting of a number of delicate subconcentric undulations. Periostracum smooth and shiny, except the posterior slope which may be roughened. Surface of the shell straw yellow to yellowish green, usually with numerous and generally fine green rays, sometimes with distinctly darker rays on the posterior slope.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Nacre bluish white and iridescent.

Length mm	Height mm	Width mm	
110	67	49	Sandpit, near Edisto River, Givhans Ferry State Park, 2 mi. NW Givhans, Dorchester Co., South Carolina.
87	50	35	Pond, near Savannah, Chatham Co., Georgia.
83	46	35	Charleston, South Carolina. Lectotype of *A. dunlapiana* Lea.
67	38	29	Hopeton, near Darien, McIntosh Co., Georgia. Lectotype of *A. couperiana* Lea.

Anatomy. Discussed by Lea (1863: 451).

Habitat. Prefers sandy or muddy bottoms of ponds and sluggish streams.

Remarks. In the Southern Atlantic Slope region, *Anodonta couperiana* Lea can be confused only with *A. imbecilis* Say. Both species have umbos which do not extend above the dorsal margin, a character which distinguishes them from the other *Anodonta* of the Atlantic Slope. *A. couperiana* is differentiated from *imbecilis* by its green rays, which are especially fine on the disk, and by its broadly curved ventral margin, which renders the shell much higher in proportion to its length than *imbecilis*, whose ventral margin is almost straight and parallel to the dorsal one. The height/length ratio of *couperiana* is about 2 to that of 1.5 in *imbecilis*.

A. couperiana is found in the Apalach-

icola River system with *A. peggyae* Johnson, which differs from *couperiana* by being subrhomboidal rather than elliptical in outline, and by being more biangulate posteriorly, with the biangulation ending near the base. *A. couperiana* is more pointed posteriorly with the point ending near the medial line. In *A. peggyae*, when the dorsal margin is held straight, the ventral margin is often obliquely descending toward the broad posterior basal biangulation.

A. couperiana is a rare species in Georgia, but the specimens from the northern part of the range are remarkable for their size and beauty. It is common and abundant in Central Florida, where individuals tend to be small.

Range. Apalachicolan region: Apalachicola, Ochlockonee, and St. Marys river systems. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Cape Fear River system, North Carolina.

Specimens Examined

Saint Marys River System

Saint Marys River Drainage. *Florida*: St. Marys River (ANSP; MZUM).

Altamaha River System

Altamaha River Drainage. *Georgia*: Rice field ditches on the Altamaha River, Hopeton, near Darien, McIntosh Co.

Savannah River System

Savannah River Drainage. *South Carolina:* Brickyard Pond, Hamburg, Aiken Co. (USNM). Savannah River [Johnsons Landing], 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *both* Allendale Co. *Georgia:* Pond near Savannah, Chatham Co.

Combahee River System

Salkehatchie River Drainage. *South Carolina:* Pauline Cave, near Kline, Barnwell Co. (ANSP).

Edisto River System

Edisto River Drainage. *South Carolina:* Sandpit, near Edisto River, Givhans Ferry State Park, 2 mi. NW Givhans, Dorchester Co. Charleston, Chatham Co. (USNM).

Cooper-Santee River System

Saluda River Drainage. *South Carolina*: Milton, Laurens Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

Genus *Strophitus* Rafinesque

Strophitus Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 316.

Type species, *Anodonta undulata* Say. Monotypic. Ortmann, 1912, Ann. Carnegie Mus., 8: 299.

Pseudodontoideus Frierson 1927, Check List North American Naiades, p. 9, 23. Instituted as a subgenus.

Type species, *Margaritana alabamensis* Lea. Original designation.

Strophitus contains two species, *undulatus* (Say), which is widely distributed throughout the Interior Basin and Atlantic Slope region, and *subvexus* (Conrad) (Johnson, 1967: 3, pl. 1, figs. 1–3), which extends from the eastern part of the West Gulf Coastal region through the Apalachicolan region. All of the taxa included by Frierson under *Strophitus s. s.* and *Pseudodontoideus* Frierson are included in the synonymy of the two species mentioned above, except for: *Strophitus undulatus tennesseensis* Frierson, which may be a geographic subspecies in the modern sense; and *Strophitus radiatus* (Conrad), which belongs under *Anodontoides radiatus* (Conrad) (Johnson, 1967: 6, pl. 2, figs. 1–4).

Generally, Frierson gave neither descriptions nor reasons for instituting new subgenera, but it is presumably on the basis of the vestigial pseudocardinal teeth found in *alabamensis* (= *subvexus*) that

he instigated *Pseudodontoideus* as a subgenus. If the present synonymy of the species is correct, *Strophitus* does not need subdivision.

Strophitus undulatus (Say)
Plate 17: 2, 3

Anodonta undulata Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 6 (no type locality, here restricted: Schuylkill River, near Philadelphia, Philadelphia Co., Pennsylvania; type, ANSP [lost]).

Anodonta pensylvanica [*sic*] Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 86 (la rivière de Schuglkill [Schuylkill], près de Philadelphie [Philadelphia Co., Pennsylvania]; holotype, Geneva Museum, figured by Delessert, 1841, Rec. Coquilles de Lamarck, pl. 13, figs. 4a, 4b).

Anodon rugosus Swainson 1822, Zool. Illustrations, ser. 1, 2, pl. 96 (United States; type [location unknown]).

Anodon arcolatus Swainson 1829, Zool. Illustrations, ser. 2, 1, pl. 18 (North America; type [location unknown]).

Alasmondonta edentula Say 1829, New Harmony [Indiana] Disseminator 2, no. 22, p. 340 (Wabash River [near New Harmony, Posey Co., Indiana]; type, ANSP [lost]).

Anodonta virgata Conrad 1836, Monography Unionidae, no. 5, back cover (Buck Creek, Clarke Co., Ohio; type ANSP [lost]).

Anodonta pavonia Lea 1836, Trans. Amer. Philos. Soc., 6: 78, pl. 21, fig. 65 (headwaters of the Little Beaver [River, Lawrence Co.], Ohio; figured holotype USNM 86514). Lea, 1838, Obs. Unio, 2: 78.

Anodonta wardiana Lea 1838, Trans. Amer. Philos. Soc., 6: 46, pl. 14, fig. 42 ([Scioto River], near Chillicothe [Ross Co.], Ohio; figured holotype USNM 86488). Lea, 1838, Obs. Unio, 2: 46.

Anodon unadilla De Kay 1843, Zool. New York, Moll., pt. 5: 199, pl. 15, fig. 228 (Unadilla River, a tributary of the Susquehanna [River system], Otsego Co., New York; type, New York Lyceum of Nat. Hist. [destroyed by fire]).

Anodonta tetragona Lea 1845, Proc. Amer. Philos. Soc., 4: 165 (Alexandria [Rapides Parish], Louisiana). Lea, 1848, Trans. Amer. Philos. Soc., 10: 82, pl. 8, fig. 25; figured holotype USNM 86682. Lea, 1848, Obs. Unio, 4: 56.

Anodonta arkansensis Lea 1852, Trans. Amer. Philos. Soc., 10: 293, pl. 29, fig. 56 (Little Arkansas River, where the road to Santa Fé crosses it [Sedgwick Co., Kansas]; figured holotype USNM 86603). Lea, 1852, Obs. Unio, 5: 49.

Anodonta shaefferiana Lea 1852, Trans. Amer. Philos. Soc., 10: 288, pl. 26, fig. 50 (Horn Lake Creek [Shelby Co.], Tennessee; figured holotype USNM 86685). Lea, 1852, Obs. Unio, 5: 44.

Alasmodon rhombica Anthony 1865, Amer. Jour. Conch., 1: 158, pl. 12, fig. 5 (Michigan; figured holotype MCZ 50296).

Anodon papyracea Anthony 1865, Amer. Jour. Conch., 1: 161, pl. 15, fig. 2 (locality unknown [Potomac River, Virginia]; figured holotype MCZ 150656).

Anodon annulatus Sowerby 1867, Conch. Iconica, 17, *Anodon*, pl. 18, fig. 67 (Hab. ?; Cuming collection in BMNH [lost]).

Anodon quadriplicatus Sowerby 1867, Conch. Iconica 17, *Anodon*, pl. 28, fig. 110 (Potomac River, [Virginia]; holotype in Walpole coll., not in BMNH, [probably lost]).

Anodonta salmonia Clessin 1873, Conch. Cab., ser. 2, 9, pt. 1: 91, pl. 24, figs. 1, 2 (Nordamerika, im Ohio-und Wabash-Fluss); *non* Lea 1838.

Strophitus undulatus ovatus Frierson 1927, Check List North American Naiades, p. 22 (Middle West [Lyon Creek, Edwards Co., Illinois]; syntype MZUM 87584).

Strophitus rugosus pepinensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 204, pl. 74, fig. 8 (Lake Pepin near Lake City [Wabasha Co.], Minnesota; holotype MZUM 209137).

Strophitus rugosus winnebagoensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 205, pl. 74, figs. 1–6 (Lake Winnebago, Long Point Island, Wisconsin; holotype MZUM [original no. Univ. of Wisconsin 943a]).

Strophitus rugosus lacustris Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 207, pl. 75, figs. 6–8 (Oconomowoc Lake, Waukesha Co., Wisconsin; holotype Univ. Illinois, Urbana Z-22073 [not seen]).

Strophitus edentulus (Say). Simpson, 1914, Cat. Naiades, 1: 345. Ortmann, 1919, Mem. Carnegie Mus., 8: 197, pl. 12, figs. 7, 8.

Strophitus undulatus (Say). Simpson, 1914, Cat. Naiades, 1: 349. Ortmann, 1919, Mem. Carnegie Mus., 8: 195, pl. 12, fig. 6. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 43, fig. 41. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 29, pl. 3, figs. 7, 8.

Description. Shell medium, seldom exceeding 90 mm in length in the Atlantic boid to subrhomboid. Valves subinflated, generally rather thin, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded, somewhat pointed

or subtruncated. Ventral margin slightly curved, occasionally incurved. Dorsal mardrainage. Outline subelliptical, long rhomgin straight, ending in a slight angle with the obliquely descending posterior margin. Hinge ligament not very prominent. Posterior ridge very rounded, but occasionally slightly angular with a trace of a secondary ridge above, ending in a slight biangulation near the base. Umbos rather full, located in the anterior third of the shell, their sculpture consisting of a few very strong ridges which turn up posteriorly where there are a few radial lirae. Surface of the shell with fine irregular growth lines, generally smooth and shiny, though sometimes covered with brownish periostracum. When not heavily covered with periostracum, the shell may be yellowish, greenish or tawny, often with greenish rays over the entire surface or on the posterior slope.

Each valve has vestiges of pseudocardinal teeth which are merely slight swellings, anterior to the umbos. The hinge plate is narrow, and slightly incurved in front of the umbos. Lateral teeth are absent. Beak cavities shallow, with muscle scars on the hinge plate; anterior adductor muscle scars distinct, posterior ones faint. Pallial line scarcely visible. Nacre bluish, straw-colored or pinkish toward the umbos.

Length mm	Height mm	Width mm	
88	55	24	Swift Creek, 3 mi. SSW Garner, Wake Co., North Carolina.
74	44	27	Turkey Creek, 8 mi. NW Edgefield, Edgefield Co., South Carolina.
47	29	17	As above.

Anatomy. Figured by Lea (1838, pl. 15, fig. 47). Discussed by Ortmann (1911: 299). The glochidia are subtriangular, with hooks, and measure 0.36 mm in length and 0.30 mm in height. They may either complete their development in the marsupia of the parent or metamorphose while parasitizing the largemouth bass, *Micropterus salmoides* (Lacépède), or northern creek chub, *Semotilus atromaculatus* (Mitchill) (Baker, 1928: 201); both extend over the entire range of *S. undulatus* (Say).

Breeding season. From July to April or May of the following year.

Habitat. Lives in small rivers and creeks in mud, sand or gravel.

Remarks. Strophitus undulatus (Say), is the only species of *Strophitus* in the Interior Basin and Atlantic Slope region. The shell has no striking characters and might be confused with species of *Anodonta*, since members of both genera lack lateral teeth. *Anodonta* have no pseudocardinals, and do have a straight hinge line; whereas *Strophitus* have vestigial pseudocardinals which appear as slight swellings anterior to the umbos, and a hinge line which is incurved in front of the umbos.

S. undulatus is replaced in the Alabama-Coosa River system and Apalachicolan region by *S. subvexus* (Conrad) (Johnson, 1967: 2) which differs from *undulatus* by being distinctly rhomboidal, having a sharper posterior ridge, and by having at least one pseudocardinal in each valve elevated slightly above the hinge line.

Strophitus undulatus might be confused with *Anodontoides radiatus* (Conrad) (Johnson, 1967: 6) in these areas, except that *radiatus* is more elliptical, has broad green rays, and each valve has a long, narrow pseudocardinal tooth which is slightly elevated and roughly parallel to the hinge line.

Clarke and Berg (1959: 43) have already discussed the necessity of discarding the name *rugosus* Swainson for this species. Ortmann (1919: 195) stated that *undulatus* was only a poorly defined variety of *edentulus* (= *rugosus*), "connected by intergrades," and that they were the same species. He retained the two names, "thus avoiding inconvenience." Since only one species of *Strophitus* occurs in the Interior Basin and Atlantic Slope region, it is clear that, by priority, *undulatus* must be used.

Range. Interior Basin: Mississippi and Ohio drainages, from Central Texas to

Lake Winnipeg, Canada. Atlantic Slope: tributary of the upper Savannah River system, South Carolina, north to the St. Lawrence River system, Canada.

Specimens Examined

Savannah River System

Savannah River Drainage. *South Carolina:* Turkey Creek, 8 mi. NW Edgefield, Edgefield Co.

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Beaverdam Creek, 4.75 mi. S Creedmoor (57); Crabtree Creek, 6 mi. NW Raleigh (38); Neuse River, Pooles Bridge; Swift Creek, 3 mi. SSW Garner (20); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. W Springhope, Nash Co.

Roanoke River System

Roanoke River Drainage. *Virginia*: Mason Creek, Salem; Roanoke River, Salem; *both* (Ortmann, 1919: 204); *both* Roanoke Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

James River System

James River Drainage. *Virginia*: Calfpasture River, Goshen (Ortmann, 1919: 204); North [= Maury] River, 2 mi. WNW Lexington; North River, Buena Vista (Ortmann, 1919: 204); *all* Rockbridge Co. James River, opposite Maidens, Goochland Co. James River, Cartersville, Cumberland Co.

York River System

South Anna River Drainage. *Virginia*: [North Fork, S Anna River] Orange, Orange Co.

Rappahannock River System

Rapidan River Drainage. *Virginia*: Rapidan River, Rapidan, Culpeper Co. (Ortmann, 1919: 204).

Rappahannock River Drainage. *Virginia:* Rappahannock River, Remington, Fauquier Co. Mountain Run, Culpeper, Culpeper Co. *both* (Ortmann, 1919: 204).

Potomac River System

Potomac River Drainage. *West Virginia:* South Branch Potomac River, Romney, Hampshire Co. (Ortmann, 1919: 204). *Pennsylvania:* Conochocheague Creek, Greencastle and Scotland; East Branch, Little Antietam Creek, Waynesboro; *both* (Ortmann, 1919: 202); *both* Franklin Co. *Virginia:* North Fork, Shenandoah River, E Woodstock, Shenandoah Co. South River, Waynesboro, Augusta Co. (Ortmann, 1919: 204). South Fork, Shenandoah River, Elkton, Rockingham Co. (Ortmann, 1919: 204). *Maryland:* Potomac River, Hancock, Washington Co. (Ortmann, 1919: 204). Potomac River, Paton Id., .75 mi. W Point of Rocks, Frederick Co. *District of Columbia:* Aqueduct Lake.

Subfamily **Lampsilinae** (Ihering 1901) Ortmann 1910

Genus *Carunculina* Baker

Toxolasma Rafinesque 1831, Continuation of Monog. Bivalve Shells River Ohio (Phila.), p. 2. Species listed: *Unio cyclips; U. cinerescens; U. lividus; U. flexus; all* Rafinesque.

Type species, *Unio lividus* Rafinesque. By elimination, Frierson, 1914, Nautilus, 28: 7. Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Mich. no. 112, pp. 54, 55, show that *U. lividus* is a *nomen dubium* and that therefore *Toxolasma* must be disregarded.

Cornuculina [*sic*] Simpson 1898, *in* F. C. Baker,[1] Bull. Chicago Acad. Sci., 3(1): 109.
Type species, *Unio parvus* Barnes. Monotypic.
Carunculina, corrected in the index and on errata sheet, and reconfirmed by Simpson, 1900, Proc. United States Natl. Mus., 22: 563.
Ortmann, 1912, Ann. Carnegie Mus., 8: 377, *partim*. (Under *Eurynia*.)

Call (1896) monographed *Carunculina*, and indicated that it included only a few very variable species, and that most of its radiation was in the Interior Basin. He probably correctly reduced to synonymy many of the taxa subsequently recognized by Simpson (1914, 1: 148–161) and Frierson (1927: 87–89).

Carunculina pulla (Conrad)
Plate 17: 4–7

Unio pullus Conrad 1838, Monography Unionidae, no. 11, p. 100, pl. 55, fig. 2 (Wateree River, South Carolina; figured type ANSP [lost]; Warm Springs, [= Hot Springs, Madison Co.], North Carolina [Tennessee River system]; probably either *Villosa vaneuxemensis* (Lea) or *Carunculina glans* (Lea) (Ortmann and Walker, 1922: 55). Conrad (1838: 101) states that this specimen was seen subsequent to the preparation of the plate. Therefore, the type locality is here restricted to the former locality.)
Lampsilis pulla (Conrad). Simpson, 1914, Cat. Naiades, 1: 160.
Carunculina patrickae Bates 1966, Occ. Papers, Mus. Zool. Univ. Michigan, no. 646, pp. 1–9, 3 text figs., 1 pl. (Savannah River at approximately mile point 134.5 U.S. Army Corps of Engineers Map [= Johnsons Landing, 10 mi. W Allendale, Allendale Co.], on the South Carolina bank; holotype MZUM 85274).
Carunculina pulla (Conrad). Johnson, 1967, Nautilus, 80: 127, pl. 10, figs. 1–4.

Description. Shell small, seldom reaching over 35 mm in length. Outline of female long obovate, of male, elliptical. Valves subinflated, generally thin, somewhat thickened anteriorly. Anterior end regularly rounded; posterior end of females more broadly rounded and subtruncated below the medial line, somewhat pointed in males. Ventral margin straight in males. In females marsupial swelling causes the margin to be somewhat convex a little posterior of the center. Dorsal margin slightly curved, forming a distinct angle with the obliquely descending posterior margin. Posterior ridge double, sometimes broadly rounded, but more often both ridges very angular. Posterior slope slightly concave. Umbos prominent, not much elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several concentric sharp ridges parallel to the growth lines, which curve upward to the posterior ridge. Periostracum generally with distinct growth lines, often satiny, generally blackish, though sometimes brownish, greenish, olivish, and with obscure very fine green rays.

Left valve with two raised triangular pseudocardinal teeth, one in front of the other, occasionally crenulate. Hinge line short and very narrow before two short, straight, lateral teeth. Right valve with one rather chunky, triangular pseudocardinal; one lateral tooth. Beak cavities shallow, with a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint. Pallial line distinct anteriorly. Nacre bluish white, pink to purplish, iridescent.

Length mm	Height mm	Width mm	
32.0	19.0	15.5	Savannah River, 10 mi. W Allendale, Allendale Co., South Carolina. Female.
22.0	13.5	10.0	As above. Male.
33.0	19.0	13.5	Wateree River, South Carolina. Male. [after Conrad].
25.0	17.0	11.0	University Lake, 1 mi. W Chapel Hill, Orange Co., North Carolina.

Habitat. Lives in shallow still water near the edges of streams and ponds, generally in mud, sometimes in sand.

Remarks. In the Atlantic Slope region

[1] H. B. Baker (1964, Nautilus, 78: 33) has pointed out that since Simpson contributed nothing in the original publication of this genus (under article 51 (c), 1964 edition of the International Code Zool. Nomen.), the authority for *Carunculina* must be F. C. Baker.

Carunculina pulla (Conrad) cannot be confused with any other species. The species of *Villosa* exhibit similar sexual dimorphism, but otherwise they are quite different from *pulla*. *Villosa delumbis* (Conrad) and *vibex* (Conrad) attain much larger size, have thinner, generally yellowish, distinctly rayed shells, whereas *pulla* is heavier for its size, blackish, and if rayed, only obscurely so. *Villosa villosa* (Lea), on the other hand, is broadly rayed, though the rays are sometimes visible only in transmitted light. *Villosa constricta* (Conrad) attains much larger size, has a similarly heavy shell, but it is shiny, has no distinct posterior ridge, and the females have a distinct "constriction" in the postbasal region.

Carunculina pulla most closely resembles *Carunculina parva* (Barnes) (= *C. paula* (Lea) Clench and Turner, 1956: 193) which is found throughout the Interior Basin and Apalachicolan region. The umbonal sculpture is similar, but *pulla* differs from *parva* by having heavy growth lines and a generally rougher periostracum; but more especially it differs by having a sharp posterior ridge, with a second, less prominent ridge above it. The posterior ridge is usually not present in typical *parva*, and when it is, it is generally not as acute as in *pulla*. Occasional specimens of *C. pulla* have an indistinct posterior ridge, as does one of the specimens figured. Nevertheless, the sharp posterior ridge is so generally present that *pulla*, with its relatively isolated distribution from *parva*, appears to be quite distinct from it. I have pointed out elsewhere (Johnson, 1967c) why it was not necessary to create a new taxon for this species.

Carunculina parva (Lea) is abundant in Black Creek, northern Florida, but no *Carunculina* have been reported from either the St. Marys or Satilla river systems, which are between Black Creek and the Altamaha River system. To the north, no *Carunculina* have been found on the Atlantic Slope beyond the Neuse River system.

It is likely that the ancestors of *C. pulla* entered the Southern Atlantic Slope region through a commingling of the headwaters of the Apalachicola and Savannah river systems.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Neuse River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, below Lumber City, Telfair Co. (H. D. Athearn).

Altamaha River Drainage. *Georgia*: [Altamaha River] Darien, McIntosh Co. (USNM).

Savannah River System

Savannah River Drainage. *South Carolina:* Savannah River, approximately mile point 134.5 (U.S. Army Corps of Engineers Map) = Johnsons Landing, 10 mi. W Allendale, Allendale Co.

Santee River System

Wateree River Drainage. *North Carolina:* [Headwaters of] Catawba River; Pfeiffers Pond; Stewarts Pond; Bissels Pond; Beaver Creek; *all* Charlotte, Mecklenburg Co. (*all* ANSP). *South Carolina*: Wateree River (Conrad).

Cape Fear River System

New Hope River Drainage. *North Carolina:* University Lake, an impoundment on Morgan Creek, 1 mi. W Chapel Hill, Orange Co.

Neuse River System

Neuse River Drainage. *North Carolina*: Neuse River, Raleigh, Wake Co. (Lea).

Genus *Villosa* Frierson

Micromya Agassiz 1852, Archiv für Naturgeschichte, 18 (1): 47. Species listed: *Unio lapillus* Say, *Margaritana fabula* Lea, *M. curreyana* Lea, *non Micromya* Rondani 1840 (Insecta).

Type species, *Unio lapillus* Say. Subsequent designation, Herrmannsen, 1852, Indicis Generum Malacozoorum, Supp. et Corr., p. 83.

Ortmann, 1912, Ann. Carnegie Mus., 8: 337. *partim.*

Villosa Frierson, 1927, Check List North American Naiades, pp. 11, 80.

Type species, *Unio villosus* Wright. Original designation.

At this writing, it is impossible to tell how many species there are in *Villosa*. Frierson (1927: 70–79) includes under *Lampsilis,* subgenus *Ligumia*, many taxa which have been included by other authors under *Micromya* (= *Villosa*). Except for the type species, the taxa listed by Frierson (1927: 80, 81) under *Villosa* are species of *Caruncula*. In spite of the state of the synonymy of this genus, it is clear that the majority of its species occur in the Interior Basin.

Villosa villosa (Wright)
Plate 17: 8, 9

Unio villosus B. H. Wright 1898, Nautilus, 12: 32 (Suwannee River [Luraville], Suwannee Co., Florida; syntype USNM 150503, figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 77, pl. 1, fig. 1, selected as lectotype by Johnson, 1967, Occ. Papers on Moll., 3: 9, pl. 8, fig. 1).

Lampsilis villosus (Wright). Simpson, 1914, Cat. Naiades, 1: 143.

Villosa villosa (Wright). Clench and Turner, 1956, Bull. Florida State Mus., 1: 213, pl. 4, fig. 2.

Description. Shell usually small in size, seldom exceeding 60 mm in length. Outline long, elliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females slightly more broadly rounded, that of males quite pointed. Ventral margin almost always broadly curved except in females where a slight marsupial swelling, somewhat posterior of the center, renders it straight or slightly convex. Dorsal margin straight, with a very slight, if noticeable, angle where it meets the obliquely descending posterior margin. Hinge ligament small. Posterior ridge broadly rounded, double in the male; obscured by a slight marsupial swelling in the female. Posterior slope slightly concave. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell with irregular growth lines, occasionally smooth and shiny, but usually covered with either rough or distinctly satiny periostracum, especially on the posterior slope. Periostracum sometimes subshiny, greenish yellow, dark greenish, or more often brownish black, the entire surface of the shell with broad green rays interspersed with narrow ones, sometimes only visible in transmitted light.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line short and narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit, the more anterior tooth quite vestigial, sometimes absent; one low lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre bluish white, occasionally yellowish white, iridescent, especially posteriorly.

Length mm	Height mm	Width mm	
57	28	18	Suwannee River, Luraville, Suwannee Co., Florida. Lectotype. Female.
56	29	20	St. Marys River, Nassau Co., Florida. Female.
51	27	20	Spring Creek, Decatur Co., Georgia. Male.

Habitat. "Limited to spring-fed streams and clear rivers," Clench and Turner (1956: 214); but their report did not include the rather acid and muddy St. Marys River.

Remarks. *Villosa villosa* (Wright) bears a resemblance to *Villosa vibex* (Conrad), which is more widely distributed and extends over the whole range of *V. villosa*, as they both show similar sexual dimorphism. In the female of *villosa* there is, in general, less tendency for the postbasal swelling to extend below the ventral margin, and if inclined to be somewhat posteriorly pointed, the point is higher. The male is pointed posteriorly as in *vibex*, but the shell is proportionately longer. *V. villosa* often has a distinctive roughened periostracum which produces a satiny luster.

Range. Apalachicolan region: Apalachicola River system, east to the St. Marys River system, Georgia. Peninsular Florida.

Specimens Examined

St. Marys River System

St. Marys River Drainage. *Georgia*: St. Marys River, Traders Hill, Charleton Co. (MZUM). *Florida:* St. Marys River, Nassau Co. (USNM).

Villosa vibex (Conrad)
Plate 17: 10, 11
Plate 18: 1–3

Unio vibex Conrad, [May] 1834, New Fresh Water Shells United States, p. 31, pl. 4, fig. 3 (Black Warrior River, South of Blount's Spring [Blount Co.], Alabama; figured holotype ANSP 56488a). Published in May, *teste* Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 243.

Unio modioliformis Lea, [August or September] 1834, Trans. Amer. Philos. Soc., 5: 97, pl. 13, fig. 40 (Santee Canal, South Carolina; probable figured holotype USNM 85029 [differs slightly from figure]). Lea, 1834, Obs. Unio., 1: 209. Published in August or September, *teste* Lea, 1854, Proc. Acad. Nat. Sci. Phila., 7: 244.

Unio exiguus Lea 1840, Proc. Amer. Philos. Soc., 1: 287 (Chattahoochee River, near Columbus [Muscogee Co.], Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 191, pl. 7, fig. 1; figured holotype USNM 84974. Lea, 1842, Obs. Unio, 3: 29.

Unio stagnalis Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 152 (inhabits mill ponds, Ogeechee River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, fig. 2; figured holotype MCZ 178778, purchased from J. H. Couper.

Unio prevostianus Lea 1852, Trans. Amer. Philos. Soc., 10: 269, pl. 19, fig. 24 (Eutowah [Etowah] River [North West], Georgia; figured holotype, C. M. Wheatley collection in ANSP [lost]). Lea, 1852, Obs. Unio, 5: 25.

Unio nigrinus Lea 1852, Trans. Amer. Philos. Soc., 10: 284, pl. 24, fig. 44 (West Florida; figured holotype USNM 86132). Lea, 1852, Obs. Unio, 5: 40.

Unio gracilior Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (Buckhead Creek [Burke Co.]; Tobesaufke [Tobesofkee] Creek near Macon [Bibb Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 56, pl. 8, fig. 38; figured holotype USNM 85088 [localities not separated]. Lea, 1858, Obs. Unio, 6: 56.

Unio rutilans Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 Othcalooga [Oothkalooga] Creek, Gordon Co.; Columbus [Muscogee Co.]; *both* Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 59, pl. 9, fig. 41; figured holotype USNM 85093 from [Oothkalooga] Creek. Lea, 1858, Obs. Unio, 6: 59.

Unio subellipsis Lea 1856, Proc. Acad. Nat. Sci. Phila., 8: 262 (creeks near Columbus [Muscogee Co.], Georgia). Lea, 1858, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 62, pl. 10, fig. 44; figured holotype USNM 85095. Lea, 1858, Obs. Unio, 6: 62.

Unio sudus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 170 (Dry Creek, near Columbus [Muscogee Co.]; Macon [Bibb Co.]; *both* Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 194, pl. 21, fig. 77; figured holotype USNM 85155 from Dry Creek. Lea, 1859, Obs. Unio, 7: 12.

Unio obfuscus Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 172 (Flint River, near Macon [Co.], Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 197, pl. 22, fig. 80; figured holotype USNM 85089. Lea, 1859, Obs. Unio, 7: 15.

Unio dispar Lea 1860, Proc. Acad. Nat. Sci. Phila., 12: 305 (Columbus [Muscogee Co.], Georgia). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 327, pl. 51, fig. 153; figured holotype USNM 85101. Lea, 1860, Obs. Unio, 8: 9.

Unio averillii Wright 1888, Proc. Acad. Nat. Sci. Phila., 40: 115, pl. 3, fig. 4 (Lake Ashby, Volusia Co., Florida; syntype figured by Simpson, 1892, Proc. United States Natl. Mus., 15: 414, pl. 56, fig. 6 [not located]). Lectotype USNM 91142,

selected by Johnson, 1967, Occ. Papers on Moll., 3: 5, pl. 7, fig. 4.

Villosa vibex (Conrad). Clench and Turner, 1956, Bull. Florida State Mus., 1: 209, pl. 4, fig. 4.

Description. Shell usually small in size, not exceeding 60 mm in length, though occasionally reaching 100 mm. Outline subelliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females more broadly rounded, somewhat pointed in males. Ventral margin straight or slightly curved in males, often slightly arcuate in females. Dorsal margin straight with a very slight, if noticeable, angle where it meets the obliquely descending posterior margin. Hinge ligament small. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with faint wrinkles and ridges. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell generally rather smooth, but roughened by periostracum posteriorly. Periostracum usually subshiny, greenish yellow, yellowish brown to almost black, the entire surface with numerous broad greenish rays, which in darker specimens can be seen in transmitted light.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line rather long and very narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit, the more anterior tooth vestigial, sometimes absent; one lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre bluish white, sometimes pinkish or purple, iridescent posteriorly.

Length mm	Height mm	Width mm	
100	48	32	Ochee Creek, about 5 mi. SE Toomsboro, Wilkinson Co., Georgia. Male.
52	29	17	Mill Race, 2 mi. N Sardis, Burke Co., Georgia. Female.
48	27	17	As above. Male.

Habitat. Lives in mud or soft sand, particularly where rich in vegetable detritus, in small rivers and creeks.

Remarks. In the Southern Atlantic Slope region, *Villosa vibex* (Conrad) can be confused with *Villosa delumbis* (Conrad) with which it is often found living. *V. vibex* has broader, less distinct, green rays which are less inclined to be broken by sharp growth rests than those of *delumbis*. Sexual dimorphism is not as strongly developed in *vibex*. The males of both species tend to be somewhat pointed posteriorly. Females of *vibex* tend to be broadly rounded, rendering the shell slightly arcuate, while the females of *delumbis* are greatly inflated, with the posterior margin subangulate dorsally and truncate below. In the Apalachicolan region, *vibex* can be confused with *Villosa lienosa* (Conrad) which is allopatric with *V. delumbis*. See *Remarks* under *Villosa delumbis* (Conrad) on p. 376.

Range. West Gulf Coastal region, Alabama-Coosa River system, and Apalachicolan region: Pearl River system, Mississippi, east to the Suwanee River system, Florida. Peninsular Florida. Southern Atlantic Slope: Altamaha River system, Georgia, north to the coastal ponds of the Cape Fear River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Tobesofkee Creek, near Macon, Bibb Co. (USNM). Flat Creek, 2 mi. S Perry, Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Tucsawatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, Fountains

Mill, 7 mi. SW Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Brushy Creek, 8 mi. NW Abbeville, Wilcox Co. House Creek, Bowens Mill, 9 mi. N Fitzgerald; Dicksons Creek, 10 mi. NE Fitzgerald; *both* Ben Hill Co.

Little Ocmulgee River Drainage. *Georgia:* Little Ocmulgee River, 7 mi. NE Cochran, Bleckley Co. Alligator Creek, 2 mi. W Alamo, Wheeler Co. Gum Swamp Creek, 1 mi. N McRae, Telfair Co.

Oconee River Drainage. *Georgia*: Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *both* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Rocky Creek, 8 mi. W Dudley; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Little Ohoopee River, 12 mi. NE Wrightsville; Little Ohoopee River, 2 mi. N Kite; Ohoopee River, 4 mi. S Wrightsville; *all* Johnson Co. Ohoopee River, Norristown, Emanuel Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Rocky Comfort Creek, 1 mi. N Louisville; Williamson Swamp Creek, Bartow; Nails Creek, 2 mi. S Bartow; Rocky Creek, 2 mi. S Wadley; *all* Jefferson Co. Barkcamp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; Buckhead Creek, 4 mi. E Vidette; Rocky Creek, 5 mi. SW Waynesboro; *all* Burke Co. Chew Mill Creek, 8 mi. W Millen, Jenkins Co.

Savannah River System

Savannah River Drainage. *Georgia*: Brier Creek, 7.5 mi. NE Wrens, Jefferson Co. Mill Race, 2 mi. N Sardis; Beaverdam Creek, 7 mi. NW Girard; *both* Burke Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Little Salkehatchee River, 4 mi. N Ehrhardt, Bamberg Co. Salkehatchee River, Broxton Bridge; Whippy Swamp Creek, 2.5 mi. NE Crocketville; *both* Hampton Co.

Edisto River System

Edisto River Drainage. *South Carolina:* Edisto River.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Lake Moultrie, Cross, Berkeley Co. (USNM). Santee Canal (Lea).

Pedee River System

Lynches River Drainage. *South Carolina:* Lynches River, 2 mi. NE Bishopville, Lee Co.

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* Lake Waccamaw, [town of] Lake Waccamaw, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Sprunts Pond [not located] (USNM); stream below Greenfield Mill Pond, Wilmington (ANSP); *both* New Hanover Co.

Villosa delumbis (Conrad)
Plate 18: 4–8

Unio delumbis Conrad 1834, New Fresh Water Shells United States, p. 35, pl. 5, fig. 3 (small streams near Cooper River, South Carolina; figured type not in ANSP [lost]).

Unio tenerus Ravenel 1834, Cat. Recent Shells Cabinet Edmund Ravenel, p. 7 (Cooper River, South Carolina) [*nomen nudum*]. Simpson 1892, Proc. United States Natl. Mus., 15: 416, pl. 58, figs. 5, 8 (South Carolina; figured syntype USNM 85030 [male]; [Savannah River], Georgia; figured syntype USNM 85032 [female]). Walker, 1919, Occ. Papers, Mus. Zool. Univ. Mich. no. 74, p. 1, pl. 1, figs. 1–6.

Unio vaughanianus Lea 1838, Trans. Amer. Philos. Soc., 6: 5, pl. 3, fig. 5 (Sawney's Creek, near [about 8 mi. NW] Camden [Kershaw Co.], South Carolina; two syntypes USNM 86106, one a bit smaller than the figure, the other with the outline of the figure, but with less prominent rays. The figure appears to be a composite.) Lea, 1838, Obs. Unio, 2: 5.

Unio ogeecheensis Conrad 1849, Proc. Acad. Nat.

Sci. Phila., 4: 153 (Ogeechee River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, figs. 3–4; figured syntype, fig. 3, MCZ 146971 purchased from J. H. Couper, selected as lectotype by Johnson, 1956, Bull. Mus. Comp. Zool., 115: 126.

Unio concavus Lea 1852, Trans. Amer. Philos. Soc., 10: 260, pl. 15, fig. 11 (Abbeville District [Savannah River drainage], South Carolina; figured holotype USNM 85154). Lea, 1852, Obs. Unio, 5: 16.

Unio proximus Lea 1852, Proc. Amer. Philos. Soc., 5: 252 (Georgia). Lea, 1852, Trans. Amer. Philos. Soc., 10: 271, pl. 20, fig. 27; figured holotype USNM 85131. Lea, 1852, Obs. Unio, 5: 27.

Unio contiguus Lea 1861, Proc. Acad. Nat. Sci. Phila., 13: 392 (Stewarts Mill Dam, Union Co., North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 199, pl. 28, fig. 268; figured holotype USNM 85120. Lea, 1863, Obs. Unio, 9: 21.

Unio genuinus Lea 1868, Proc. Acad. Nat. Sci. Phila., 20: 161 (Bissels Pond, Charlotte [Mecklenburg Co.] North Carolina). Lea, 1868, Jour. Acad. Nat. Sci. Phila., ser. 2, 6: 305, pl. 46; fig. 117, figured holotype USNM 85123. Lea, 1869, Obs. Unio, 12: 64.

Description. Shell usually small in size, seldom exceeding 60 mm in length. Outline of female long obovate; of male long elliptical. Valves subinflated, generally thin and translucent. Anterior end regularly rounded; posterior end of females more broadly rounded and subtruncated below the medial line, somewhat pointed in males. Ventral margin straight in males, in females marsupial swelling causes the margin to be somewhat convex a little posterior of the center. Dorsal margin straight forming a sharp angle with the obliquely descending posterior margin. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with faint ridges and wrinkles. Umbos moderately swollen, slightly elevated above the hinge line, located in the anterior third of the shell, their sculpture consisting of several fine, low, slightly double-looped ridges. Surface of the shell generally rather smooth and shiny, but roughened by periostracum posteriorly especially on the posterior slope. Periostracum often subshiny, greenish yellow, brownish, or greenish, the entire surface with narrow, sometimes very narrow, greenish rays which are broken by growth rests to form concentric bands.

Left valve with two delicate pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one inclined to be vestigial. Hinge line rather long and very narrow before two short, straight lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a narrow pit; the more anterior tooth vestigial, sometimes absent; one lateral tooth. Beak cavities shallow, a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line distinct anteriorly. Nacre sometimes dirty white or pinkish, but usually bluish white and iridescent.

Length mm	Height mm	Width mm	
64	39	30	Ogeechee River, Georgia. Lectotype of *U. ogeecheensis* Conrad. Female.
57	35	19	Mill Race, 2 mi. N Sardis, Burke Co., Georgia. Female.
53	30	19	As above. Male.

Habitat. Lives in mud or soft sand, particularly where rich in vegetable detritus, in small rivers and creeks.

Remarks. In the Southern Atlantic Slope region, *Villosa delumbis* (Conrad) can be confused only with *Villosa vibex* (Conrad) under which see: *Remarks* on p. 374.

Villosa delumbis (Conrad) is very close to *Villosa lienosa* (Conrad) of the Apalachicolan region. Both species are similarly shaped and the females show the same sexual dimorphism. *V. lienosa* has a much heavier shell; the posterior ridge, while rounded, tends to be faintly biangulate. The periostracum is usually black or very dark yellowish green, and when visible the rays are solid green. The nacre is often pinkish or coppery. *V. delumbis* has a thinner shell, there is scarcely ever a hint

of the posterior ridge being faintly biangulate, the periostracum is usually a light yellow or light greenish yellow, and the rays are almost always distinct and characteristically broken by growth rests. The nacre is very seldom pinkish.

Although the figured type of *V. delumbis* has been lost, the life size figure, with its distinct, narrow rays, clearly distinguishes it from *vibex*, and it corresponds almost exactly in outline with the male shell figured in this report.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Neuse River system, North Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Macon, Bibb Co. Echeconnee Creek, Echeconnee, Houston Co. Buck Creek, 5 mi. NW Hawkinsville; Limestone Creek, 4.3 mi. E Hawkinsville; Tucsawhatchee Creek, 5 mi. SW Hawkinsville; Cedar Creek, 8 mi. SW Hawkinsville; *all* Pulaski Co.

Oconee River Drainage. *Georgia*: Ochee Creek, about 5 mi. SE Toomsboro; Turkey Creek, 4 mi. NE Allentown; *both* Wilkinson Co. Ford Branch, 4 mi. W Dublin; Palmetto Creek, 7 mi. S Dublin; *both* Laurens Co.

Ohoopee River Drainage. *Georgia*: Ohoopee River, 4 mi. S Wrightsville; Little Ohoopee River, 1 mi. E Kite; *both* Johnson Co. Ohoopee River, 1 mi. E Adrian; Ohoopee River, Norristown; Yam Grande Creek, 3 mi. W Swainsboro; *all* Emanuel Co.

Altamaha River Drainage. *Georgia*: Darien, McIntosh Co. (USNM).

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee River, 4 mi. SW Mitchell, Glascock Co. Williamson Swamp Creek, Bartow, Jefferson Co. Barkcamp Creek, 7 mi. E Midville; Mill Creek, 5 mi. E Midville; *both* Burke Co. Chew Mill Creek, 8 mi. W Millen, Jenkins Co. Ogeechee River, Scarboro; Ogeechee River, bridge 1 mi. S Dover; Ogeechee River, 1.5 mi. SW Oliver; *all* Screven Co. (*all* MZUM). Ogeechee River, bridge 1.5 mi. E Blitchton; Ogeechee River, Jinks Bridge [Rte. 16]; Ogeechee River, Morgan Bridge, 14 mi. SE Pembroke; Ogeechee River, mouth of Arnold Lake; Jones Lake; *all* Bryan Co. (*all* MZUM).

Savannah River System

Broad River Drainage. *Georgia*: Broad River, Elbert, Huguenot Co. (USNM) Broad River, Lincoln Co.

Savannah River Drainage. *Georgia*: Savannah River, Augusta, Richmond Co. *South Carolina:* Savannah River, 2 mi. SW Millettville (MZUM); Savannah River, Johnsons Landing, 10 mi. W Allendale; *both* Allendale Co. *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Brier Creek, 6 mi. N Waynesboro; outlet of Waynesboro Lake, Waynesboro; Mill Race, 2 mi. N Sardis; *all* Burke Co.

Combahee River System

Salkehatchee River Drainage. *South Carolina:* Pauline Cave, near Kline, Barnwell Co. (MZUM).

Edisto River System

Edisto River Drainage. *South Carolina:* Snake Swamp Creek, Orangeburg Co. 6 mi. NE Bamberg, Bamberg Co. Edisto River, Canadys Landing, 8 mi. SW St. George, Dorchester Co. Edisto River, 1 mi. E Jacksonboro, Colleton Co. (MZUM).

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Catawba River Drainage. *North Carolina:* Long Creek; Catawba River; Bissels Pond, Charlotte; Pfeiffers Pond, Charlotte (ANSP); Flannigans Pond, Charlotte (ANSP); *all* Mecklenburg Co. [Ten Mile

Creek] of Catawba River, Wolfsville [7 mi. W Monroe], Union Co. (MZUM).

Wateree River Drainage. *South Carolina:* Sawneys Creek, about 8 mi. NW Camden, Kershaw Co. (USNM).

Cooper River Drainage. *South Carolina:* near Cooper River (Conrad).

Pedee River System

Yadkin River Drainage. *North Carolina:* Stewarts Mill Dam, Union Co. (USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina:* drainage canal beside Lake Waccamaw, 1 mi. NNW Dupree Landing, Columbus Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina*: University Lake, an impoundment on Morgan Creek, 1 mi. W Chapel Hill, Orange Co. Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM). North East Cape Fear River, Dublin Co. (MZUM). Greenfield Mill Pond, Wilmington, New Hanover Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro Center, Person Co. (81). Neuse River (USNM).

Villosa constricta (Conrad)
Plate 18: 9–10

Unio lienosus constrictus Conrad 1838, Monography Unionidae North America, no. 10, p. 91, pl. 49, fig. 4 (North [= Maury] River, Rockbridge Co., Virginia; figured holotype ANSP 20423, now ANSP 56465a.)

Unio genthii Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (Catawba River, Gaston Co.; Deep River, Gulf [Chatham Co.]; *both* North Carolina). Lea, 1862, Jour. Acad. Nat. Sci. Phila., ser. 2, 5: 57, pl. 2, fig. 204; figured holotype USNM 84834, labeled, Roanoke River, Raleigh, North Carolina, Prof. Emmons. (This locality is nonexistent. There is no way to tell which locality the type was from; so it is assumed here that since it was probably Prof. Emmons' specimen that was figured, it was from Deep River, Gulf, Chatham Co., North Carolina, and the type locality is, here, so restricted.) Lea, 1862, Obs. Unio, 8: 61.

Lampsilis constricta (Conrad). Simpson, 1914, Cat. Naiades, 1: 111.

Eurynia (*Micromya*) *constricta* (Conrad). Ortmann, 1915, Nautilus, 29: 66.

Description. Shell small in size, seldom exceeding 50 mm in length. Outline of female short obovate; of male subelliptical. Valves not much inflated, rather heavy and strong. Anterior end regularly rounded; posterior end of females more broadly rounded and pointed a little more than midway up from the base, truncated below the medial line. In mature specimens there is a rather distinct "constriction" in the middle of this truncation which marks the boundary between the branchial opening and the papillar part of the mantle edge in front of it; somewhat pointed in males, the point being generally less than midway up from the base. Ventral margin quite convex in females, slightly convex in males. Dorsal margin rather rounded, forming a more or less distinct angle with the obliquely descending posterior margin. Posterior ridge broadly rounded. Posterior slope slightly concave, occasionally with fine radiating wrinkles. Umbos not much swollen, slightly elevated above the hinge line, located in the anterior quarter of the shell, their sculpture consisting of evenly double-looped ridges. Surface of the shell generally rather smooth and shiny, sometimes roughened with concentric growth lines. Periostracum often subshiny, yellowish green, or bottle green, becoming brownish with age, generally with distinct, but very fine, green rays over the entire surface.

Left valve with two rather heavy pseudocardinal teeth, one in front of the other, both rather triangular. Hinge line very short and very narrow before two straight lateral teeth. Right valve with two pseudocardinals, the posterior one chunky and serrated, the more anterior tooth vestigial; one lateral tooth. Beak cavities shallow,

a few dorsal muscle scars under the hinge plate. Anterior adductor muscle scars well impressed, posterior ones faint, if visible. Pallial line generally distinct anteriorly. Nacre sometimes dirty white or yellowish, especially toward the beak cavities, but usually bluish white and iridescent.

Length mm	Height mm	Width mm	
49.0	28.0	17.0	Pedlar River, 1 mi. W Pleasantview, Amherst Co., Virginia. Male.
41.4	27.0	16.0	North River, Rockbridge Co., Virginia. Female. Holotype of *Unio constrictus* Conrad.
39.0	27.0	18.0	[Deep River, Gulf, Chatham Co.], North Carolina. Male. Holotype of *Unio genthii* Lea.

Breeding season. The breeding season begins in August and ends in June. Glochidia subspatulate, higher than long. Length 0.21 mm, height 0.27 mm (Ortmann, 1915: 66, 67).

Habitat. Lives in sand in rather swift, flowing rivers.

Remarks. Villosa constricta (Conrad) of the Southern Atlantic Slope region does not much resemble any other unionid found there. There is often quite a bit of difference in the degree of inflation and form of the shell, but it differs from all of the other Atlantic Slope *Villosa* in the shape of the postbasal swelling which generally does not project beyond the base line of the shell, and in the emargination behind the swelling. For its size *constricta* is much heavier and stronger than any other *Villosa* in the region under study, and has a distinctive yellowish green or shiny dark chestnut-brown periostracum, and the female has a distinct constriction in the postbasal region. Females of *Carunculina pulla* (Conrad) show a similar sexual dimorphism, but they lack the constriction. In addition, *pulla* usually has a sharp double posterior ridge, a rough periostracum and if rayed at all, obscurely so, whereas *constricta* has a broadly rounded posterior ridge and a generally smooth, shiny surface that is distinctly rayed.

Villosa constricta (Conrad) is allopatric with *Villosa vanuxemensis* (Lea) (Simpson, 1914, 1: 105) of the Cumberland and Tennessee rivers. The constriction found rather regularly in old females of *constricta* is not as well developed in *vanuxemensis*, and the latter has a distinct nacre color (usually an unreliable character) which varies from dirty purplish white through salmon-tinted to dark purple, usually darker toward the beak cavity of the shell, whereas the nacre color of *constricta* is dirty white, bluish white or yellowish toward the beak cavities. Ortmann (1915: 66) collected a number of specimens of *vanuxemensis* on September 17, 1912 in the North Fork, Holston River, Saltville, Smyth Co., Virginia, and at once recognized its affinity with *constricta*.

Range. Southern Atlantic Slope: Catawba River, North Carolina, of the upper Cooper-Santee River system, north to the James River system, Virginia.

Specimens Examined

Cooper-Santee River System

Catawba River Drainage. *North Carolina:* Catawba River, Gaston Co. (Lea). Beaver Creek [Gaston Co.] (MZUM). Long Creek [Mecklenburg Co.] (MZUM). [Ten Mile Creek] of Catawba River, Wolfsville [7 mi. W Monroe], Union Co. (USNM).

Cape Fear River System

Deep River Drainage. *North Carolina*: Deep River, Gulf, Chatham Co. (Lea).

Cape Fear River Drainage. *North Carolina:* Rocky River, 11 mi. N Sanford, Chatham Co. (MZUM).

Neuse River System

Neuse River Drainage. *North Carolina*: North Flat River, 5.5 mi. S Roxboro, Person Co. (81). Eno River, 1.8 mi. S Cedar Grove (122); Eno River, Hillsboro; *both*

Orange Co. Eno River, 6 mi. NW Durham (113); Fork, Little River, 11 mi. NNW Durham (101); *both* Durham Co. Neuse River, 6 mi. E Raleigh; Hare-Snipe Creek, 6.25 mi. NW Raleigh (37); Little River, Tarpleys Mill, 2 mi. NE Wendell (5); *all* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. ENE Bunn, Franklin Co. Chicod Creek, Pitt Co. (MZUM).

Roanoke River System

Staunton River Drainage. *Virginia*: Mason Creek, near Roanoke River, Salem; Tinker Creek, Roanoke (MZUM); *both* Roanoke Co.

James River System

James River Drainage. *Virginia*: Dunlap Creek (MZUM); Jackson River, Covington (MZUM); Cowpasture River, near Longdale (MZUM); *all* Alleghany Co. Calfpasture River, Goshen (MZUM); North [= Maury] River, 2 mi. WNW Lexington; *both* Rockbridge Co. James River, Buchanan, Botetourt Co. Pedlar River, 1 mi. W Pleasantview, Amherst Co. James River, opposite Beaver Creek, 6 mi. E Lynchburg, Campbell Co. (MZUM). James River, Cartersville, Cumberland Co. James River, opposite Maidens, Goochland Co. James River, Richmond, Henrico Co. (ANSP).

Genus *Ligumia* Swainson

Ligumia Swainson 1840, Treatise on Malacology, pp. 268, 274, 378.

Type species, [*Unio*] *recta* Lamarck. Original designation, p. 274.

Ortmann, 1912, Ann. Carnegie Mus., 8: 338, *partim*.

Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Mich., no. 112, p. 59.

Frierson (1927: 70–79) includes many taxa in this genus. Most of them have been placed by subsequent authors under *Lampsilis s. s.* and *Villosa*. It appears that *Ligumia* contains two species, *L. recta* (Lamarck) (Ortmann, 1919: 276, pl. 16, figs. 12, 13) (the so-called subspecies *latissima* (Rafinesque) is an ecophenotype, occurring in rivers) and *L. nasuta* (Say).

Ligumia nasuta (Say)
Plate 19: 1, 2

Unio nasutus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 4, fig. 1 (Delaware and Schuylkill [rivers near Philadelphia, Philadelphia Co., Pennsylvania]; type, ANSP [lost]).

Obliquaria attentuata Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 304 (la fleuve Hudson [New York]; type, not in ANSP [lost]).

Unio rostrata Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, pt. 2, 2: 233, pl. 53, fig. 3 (Philadelphia vicinis [near] [Philadelphia Co., Pennsylvania]; type [location unknown]).

Unio vaughanianus Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 61, fig. 308, *non* Lea, 1838.

Unio fisherianus Kuester 1860, Conch. Cabinet, 9, pt. 2, pl. 68, fig. 6, *non* Lea, 1838.

Lampsilis nasuta (Say). Simpson, 1914, Cat. Naiades, 1: 97.

Eurynia nasuta (Say). Ortmann, 1919, Mem. Carnegie Mus., 8: 271, pl. 16, figs. 10, 11.

Ligumia nasuta (Say). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. 367, p. 51, fig. 54.

Description. Shell generally medium in size throughout most of its range, usually not exceeding 80 mm in length, though reaching over 110 mm in a few localities. Outline elongated, subelliptical, or sublanceolate; distinctly over twice as long as high. Valves usually subcompressed, thin to subsolid, inequilateral. Anterior end regularly rounded; posterior end elongated and bluntly pointed. Ventral margin curved. Dorsal margin straight, slightly curved, forming a distinct angle, at least in immatures, with the obliquely descending posterior slope. Hinge ligament rather long and low. Posterior ridge distinct and angular, becoming toward the umbos broader, more rounded, and indistinct. Posterior slope slightly concave, near the umbos becoming flatter or even somewhat

convex posteriorly. Umbos very low, located in the anterior quarter of the shell, their sculpture consisting of fine close ridges which are looped in front and run parallel to the axis of the shell behind. Surface of the shell with irregular growth lines, sometimes with a few nearly vertical ridges below the posterior ridge. Periostracum usually fine, subshiny, greenish yellow, dark olive to brownish, often with distinct fine rays, especially posteriorly.

Left valve with two compressed pseudocardinal teeth, one in front of the other, both subtriangular and crenulated; no interdentum; two long straight laterals. Right valve with two pseudocardinals, the posterior one triangular, the more anterior one low and vestigial; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior adductor muscle scars well impressed; posterior ones often scarcely visible. Pallial line distinct anteriorly. Nacre bluish white, often cream color or salmon, especially toward the beak cavity, posteriorly iridescent.

Sexual differences well marked in the shell. The male shell tapers uniformly behind into a point, but the female is distinctly produced in the postbasal region, behind which the ventral margin slopes up more acutely than in the male, and is straight or concave.

Length mm	Height mm	Width mm	
112	44	28	Connecticut River, Hartford, Hartford Co., Connecticut. Male.
66	29	14	Potomac River, Washington, District of Columbia. Female.
62	25	12	As above. Male.

Anatomy. Discussed by Ortmann (1911: 343); discussed and figured by Reardon (1929: 7, pl. 2, figs. 1–10). The glochidia are subovate, with an undulate hinge line, and measure 0.25 mm in length and 0.29 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 272) indicates from specimens he examined in Lake Erie that this species breeds from August until the following June.

Habitat. Lives in sand and mud, mostly in protected areas in ponds, lakes, canals, and in slack water areas of streams.

Remarks. Ligumia nasuta (Say) of the upper Ohio River drainage and Atlantic Slope region is distinguishable from any other North American unionid by its usually distinctly lance-head shaped posterior end. On the Atlantic Slope the male shell can be confused with *Elliptio lanceolata* (Lea), but the latter does not have the same distinct pattern of rays, nor the dull olive green color. Also the nacre of *nasuta* is generally silvery white or cream colored, whereas that of *lanceolata* may be coppery or purple. The females of *nasuta* have a distinct expansion in the postbasal region which render them more easily distinguishable from *lanceolata* than the male shell.

Clarke and Berg (1959: 51), apparently following Simpson (1914, 1: 97), give the southern range of this species as North Carolina. Simpson's record appears to be based on series of rather posteriorly produced specimens of *Elliptio lanceolata* (Lea) from Wilmington, New Hanover Co., North Carolina. *Ligumia nasuta* is decidedly part of the northern element of the Atlantic Slope fauna, the James River, Virginia, being its southernmost record. (Conrad, 1836: 38, pl. 18, fig. 1, figures a female specimen from the James River, but it has not been collected there since his time.) As observed by Conrad, *nasuta* does not go very far up into the rivers in the southern part of its range, and we are led by Conrad to believe that his record from the James is from the tidewater region. It is abundant in the Potomac River in the tidewater region, but is not found very far up the river. Ortmann (1919: 275) found the distribution to be similar in Pennsylvania.

Range. Atlantic Slope: James River system, Virginia, north to the St. Lawrence

River system, Canada, westward through the Mohawk River and Erie [now New York State Barge] Canal, *both* New York. Interior Basin: Lake Erie, Ohio, and Michigan.

Specimens Examined

James River System

James River Drainage. *Virgina*: James River (Conrad).

Potomac River System

Potomac River Drainage. *District of Columbia:* Potomac River.

Genus *Lampsilis* Rafinesque

Lampsilis Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 298. Species listed: *Lampsilis cardium* Rafinesque, *Lampsilis ovata* (Say), *Lampsilis fasciola* Rafinesque.

Type species, *Unio ovatus* Say. Subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum, 1: 575. Ortmann, 1912, Ann. Carnegie Mus., 8: 345.

Aeglia Swainson 1840, Treatise on Malacology, pp. 265, 378. Species listed: *Ae. ovata* (Say), *occidens* (Lea).

Type species, *Unio ovatus* Say. Subsequent designation, Herrmannsen, 1846, Indicis Generum Malacozoorum, 1: 20.

Subgenus *Lampsilis s.s.*

All of the species described in this paper belong to *Lampsilis s. s.* Frierson (1927: 67–86) lists ten other subgenera, three of which are of his own creation. One of them, *Villosa*, is now used as a replacement name for *Micromya* Agassiz (see under *Villosa* on p. 371. *Ligumia* Swainson now replaces *Eurynia* Rafinesque. To comment on the other subgenera is not in the scope of this paper, but on cursory examination, the present author disagrees substantially with Frierson's classification, both on a generic and specific level.

Lampsilis s. s., while clearly of Interior Basin origin, appears to have speciated about equally there and in the combined Apalachicolan and Atlantic Slope regions.

Lampsilis (Lampsilis) cariosa (Say)
Plate 19: 3–5

Unio cariosus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3, fig. 2 (Delaware and Schuylkill Rivers; [Susquehanna River], Wilkes Barre; [Luzerne Co.; *all* Pennsylvania]; type, ANSP [lost]). The type locality was restricted to: Schuylkill River, near Philadelphia, Pennsylvania, and a neotype MCZ 178839 was selected by Johnson (1947, Occ. Papers on Moll., 1: 148, pl. 19, fig. 1).

Lampsilis pallida Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 299 (Hudson River, [New York]; type not in ANSP [lost]).

Unio ovata Valenciennes 1827, *in* Humboldt and Bonpland, Voyage aux Régions Equinoxiales du Nouveau Continent, pt. 2, 2: 226, pl. 50, figs. 1 a–c, (près de Washington [District of Columbia]; type [location unknown]) *non* Say 1817.

Unio crocatus Lea 1841, Proc. Amer. Philos. Soc., 2: 31 (Savannah River, Georgia). Lea, 1842, Trans. Amer. Philos. Soc., 8: 238, pl. 22, fig. 52; figured holotype USNM 84908. The lectotype selected by Johnson (1947, Occ. Papers on Moll., 1: 156) but not figured, is invalid. The holotype which was catalogued under the same number has since been located. Lea, 1842, Obs. Unio, 3: 76.

Unio oratus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 153 (Flint River, Georgia; here restricted to: Ogeechee River, Georgia[1]). Conrad 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 267, pl. 37, fig. 6; type, coll. of J. H. Couper [lost].

Lampsilis cariosa (Say). Simpson, 1914, Cat. Naiades, 1: 43. Ortmann, 1919, Mem. Carnegie Mus., 8: 313, pl. 20, figs. 3–5. Johnson, 1947, Occ. Papers Moll., 1: 145, pl. 19, figs. 1–2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 54, figs. 59–60. Clarke and Rick, 1963, Natl. Mus. Canada, Bull. no. 189, p. 27, pl. 1, fig. 3.

Description. Shell usually medium, though reaching 130 mm in length. Outline of male elliptical and somewhat elongate; of female subovate, or obovate, rather short and high. Valves inequilateral, some-

[1] Also described on the same page in both publications is *Unio contrarius* = *Lampsilis claibornensis* (Lea) with Ogeechee River, Georgia, as the type locality. The localities for the two species are obviously transposed, since *oratus* is not found in the Flint River, but in the Ogeechee River, and *contrarius* is found in the Flint River and not in the Ogeechee River.

what inflated; moderately heavy. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly curved. Dorsal margin straight, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rounded and poorly defined. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five wavy recurved ridges. Surface of the shell generally smooth except for a few growth ridges. Periostracum usually shiny, bright wax or straw yellow, infrequently greenish yellow, becoming a dirty brownish yellow or reddish brown in matures. Green or blackish rays, when present, usually restricted to the posterior slope.

Left valve with two compressed, serrated pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, but chunky, located directly under the umbo. Hinge line rounded, with a considerable interdentum under the umbo before two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, chunky and serrated; one lateral tooth, sharply truncated behind. Beak cavities moderately deep, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre bluish white or tinged with salmon.

Length mm	Height mm	Width mm	
130	85	56	Savannah River, 7 mi. NE Newington, Screven Co., Georgia. Male.
98	62	42	As above. Male.
98	69	45	As above. Female.

Anatomy. Figured by Lea (1838, pl. 15, fig. 45). Ortmann (1912: 353) says that the anatomy of *L. cariosa* is similar to that of *Lampsilis ovata ventricosa* (Barnes).

Breeding season. According to Ortmann (1919: 315) this species is probably brady-tictic.

Habitat. The largest examples are found in the swift waters of large rivers on sand bars or gravelly bottoms, though it also occurs in smaller creeks and, occasionally, in ponds.

Remarks. In the Atlantic Slope region, *Lampsilis cariosa* (Say) can be confused with *L. dolabraeformis* (Lea) of the Altamaha River system, but the latter species has much higher umbos and a very sharp posterior ridge, especially toward the umbos, whereas in *cariosa* the umbos are slightly elevated above the hinge line, and the posterior ridge is poorly defined.

Lampsilis cariosa has been most often confused with *L. ochracea* (Say) with which it is sometimes found throughout its range. In general, *L. ochracea* has a thinner, smaller shell, and unlike *cariosa*, which is rarely rayed except posteriorly, *ochracea* is often rayed over the entire surface of the shell and it has a rougher, duller, more greenish periostracum. The hinges are quite different. The pseudocardinals of *L. cariosa* are pyramidal, and an interdentum is present; but in *L. ochracea* the pseudocardinals are lamellate, almost parallel to the hinge line, and there is no interdentum.

Lampsilis cariosa is found with *Lampsilis ovata* (Say) in the Potomac River system, where the latter was introduced, and in the St. Lawrence River system. While the two species are close, they are distinct. *L. ovata* has a rather sharp posterior ridge, is somewhat inflated, has a dull olivaceous tint to the shell, and is inclined to be rayed over the entire surface. *L. cariosa* has a poorly defined posterior ridge, is not especially inflated, usually has a distinctive bright yellow, glossy periostracum, and rays when present are usually confined to the posterior slope.

Range. Atlantic Slope: Ogeechee River system, Georgia, north to the Sydney River, Nova Scotia (Clarke and Rick, 1963: 27), and in the St. Lawrence River system, Canada, westward to the Madawaska River, Ontario, of the lower Ottawa River drainage.

Specimens Examined

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Ogeechee River, Shoals, Warren Co. Ogeechee River, Scarboro, Screven Co. (MZUM). Ogeechee River, mouth of Arnold Lake [Bryan Co.] (MZUM).

Savannah River System

Savannah River Drainage. *South Carolina:* Abbeville District (USNM). Edgefield District. Savannah River, 2 mi. SW Millettville (ANSP); Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale (ANSP); *all* Allendale Co. *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Savannah River, 6 mi. NE Girard; *both* Burke Co. Below Haga Slage Landing, E Sylvania (ANSP); Savannah River, 7 mi. NE Newington; *both* Screven Co. Savannah River, in sandbank, Savannah, Chatham Co. (MZUM).

Cooper-Santee River System

Congaree River Drainage. *South Carolina:* Congaree River.

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina:* Santee River, Wilsons Landing, 5 mi. NW Pineville (ANSP); below Santee River Dam, near St. Stephens; *both* Berkeley Co.

Waccamaw River System

Waccamaw River Drainage. *South Carolina:* Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Cape Fear River, Cumberland Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Eno River, 6 mi. NNW Durham, Durham Co. (112). Neuse River [6 mi. E] Raleigh; tributary of Swift Creek, 5 mi. SW Raleigh (22); *both* Wake Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, 2 mi. W Springhope, Nash Co.

Chowan River System

Nottoway River Drainage. *Virginia*: Nottoway River, 3 mi. E Rawlings, Brunswick Co.

York River System

Pamunkey River Drainage. *Virginia*: Pamunkey River, 2 mi. N Hanover, Hanover Co.

Potomac River System

Potomac River Drainage. *Maryland*: Monocacy River, 2 mi. W Mt. Pleasant, Frederick Co. Potomac River, Cabin John, Montgomery Co. (Ortmann, 1919: 316). Potomac River, Great Falls, Fairfax Co. *District of Columbia:* Potomac River.

Lampsilis (Lampsilis) dolabraeformis (Lea)

Plate 20: 1–4

Unio dolabraeformis Lea 1838, Trans. Amer. Philos. Soc., 6: 103, pl. 24, fig. 113 (Altamaha River, Liberty [now Long] Co.; Altamaha River, near Darien [McIntosh Co]; *both* Georgia; figured holotype USNM 84888). Lea, 1838, Obs. Unio, 2: 103.

Lampsilis dolabraeformis (Lea). Simpson, 1914, Cat. Naiades, 1: 46.

Description. Shell large, often exceeding 130 mm in length. Outline of male

elliptical and somewhat elongate; of female obovate, rather short and high. Valves inflated, rather heavy. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly curved. Dorsal margin straight, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge very sharp and angular near the umbos, gradually becoming less so toward the ventral margin, especially in older individuals. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos swollen, much elevated above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five rather evenly raised bars which terminate at the posterior ridge. Surface of the shell smooth except for a few concentric ridges anteriorly. Periostracum usually shiny, yellowish green, sometimes becoming chestnut brown or black in matures. The posterior slope usually has a concentration of green or black rays which extend with less frequency over the posterior portion of the disk.

Left valve with two compressed pseudocardinal teeth, one in front of the other, the anterior one higher. Sometimes these are broken into three imperfect teeth or are united in one narrow ridge. Hinge line rounded, with a considerable interdentum under the umbo before two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, chunky, and serrated; one lateral tooth, sharply truncated behind. Beak cavities deep and wide, with deep dorsal muscle scars under the pseudocardinal teeth. Anterior adductor muscle scars deep, posterior ones distinct, but not impressed. Pallial line distinct. Nacre white, bluish white, or pinkish, usually iridescent.

Length mm	Height mm	Width mm	
129	91	64	Altamaha River, 4 mi. N Jesup, Wayne Co., Georgia. Male.
108	78	55	As above. Female.
91	69	49	Altamaha River, 10 mi. N Baxley, Appling Co., Georgia. Female.
79	63	50	As above. Male.

Anatomy. Discussed by Lea (1863: 413).

Habitat. Usually found in sand bars, where the river is wide and the water is rather swift, though occasionally found in mud.

Remarks. Lampsilis dolabraeformis (Lea) is known only from the Altamaha River system. It is close to *Lampsilis cariosa* (Say) which is found throughout the Atlantic Slope region, but differs from *cariosa* by having umbos which are much higher and a posterior ridge which is considerably sharper, especially toward the umbos.

In the Apalachicolan region, *L. dolabraeformis* resembles *L. excavatus* (Lea). The latter does not extend east of the Escambia River system. It is a smaller species than *dolabraeformis*, the umbos are not as high, the posterior ridge is not quite as sharp, especially in females, and the entire surface has wide green or blackish rays which are often broken into concentric bands of green. In *dolabraeformis* the rays are restricted to the area toward the posterior ridge and posterior slope, and the rays are fine, sharp, and not broken. *L. dolabraeformis* also resembles *L. binominatus* Simpson (Johnson, 1967b: 9) of the Upper Apalachicola River system. The rays are very similar, but in *binominatus* they cover the entire surface. Further, *binominatus* is a much smaller species, which does not have the high umbos or sharp posterior ridge of *dolabraeformis*.

Simpson (1914, 1: 46) reports *dolabraeformis* from the Ogeechee and Savannah River systems, but the specimens in the United States National Museum are all *Lampsilis cariosa* (Say).

Range. Southern Atlantic Slope: restricted to the Altamaha River system, Georgia.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Ocmulgee River, Hawkinsville, Pulaski Co. Ocmulgee River, 1.5 mi. S Jacksonville; Gum Swamp Creek, 1 mi. N McRae; Ocmulgee River, 1 mi. S Lumber City; *all* Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood; Ochwalkee Creek, 2 mi. E Glenwood; Oconee River, 8 mi. SW Soperton; *all* Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Hazlehurst, Jeff Davis Co. Altamaha River, 10 mi. N Baxley; Altamaha River, 10 mi. NE Surrency; *both* Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Lampsilis (Lampsilis) ovata (Say)
Plate 21: 1–2

Unio ovatus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 2, Fig. 7 (Ohio River and its tributary streams; type, ANSP [lost]). Neotype Senckenberg Mus. 4338 [not seen] selected, but not figured, by Haas, 1930, Senckenbergiana, 12: 328.

Lampsilis cardium Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 298, pl. 30, figs. 16–19; ([Ohio River]: supposed type ANSP 20210 *teste* Vanatta, 1915, Proc. Acad. Nat. Sci. Phila., 66: 5511).

Unio ventricosus Barnes 1823, Amer. Jour. Sci., 6: 267, pl. 13, fig. 14 (The Wisconsan [Wisconsin River] near Prairie du Chien [Crawford Co., Wisconsin] type, Lyceum of Natural History of New York [destroyed by fire]).

Unio occidens Lea 1829, Trans. Amer. Philos. Soc., 3: 435, pl. 10, fig. 16 (Ohio; figured holotype USNM 84866). Lea, 1834, Obs. Unio, 1: 49.

Unio subovatus Lea 1831, Trans. Amer. Philos. Soc., 4: 118, pl. 18, fig. 46 (Ohio River; figured holotype USNM 84509). Lea, 1834, Obs. Unio, 1: 128.

Unio lenis Conrad 1838, Monography Unionidae, no. 11, back cover. Conrad, 1840, *op. cit.*, no. 12, p. 106, pl. 58, fig. 2 (upper part of White River, Illinois, possible type ANSP 42307, [smaller than figured specimen]).

Unio canadensis Lea 1857, Proc. Acad. Nat. Sci. Phila., 9: 85 (St. Lawrence River, near Montreal [Quebec], Canada). Lea, 1860, Jour. Acad. Nat. Sci. Phila., ser. 2, 4: 268, pl. 44, fig. 148; figured holotype USNM 84503. Lea, 1860, Obs. Unio, 7: 86.

Unio latissimus Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 66 fig. 337 (United States, Sowerby coll. not in BMNH [lost]).

Lampsilis ventricosa lurida Simpson 1914, Cat. Naiades, 1: 41 (throughout the St. Lawrence drainage; holotype USNM [not located]).

Lampsilis ventricosa cohongoronta Ortmann 1912, Nautilus, 26: 53 (no type selected. Lectotype, selected by Parodiz (1967: 28) Carnegie Mus. 61.3999, from Potomac River, Hancock, Washington Co., Maryland), pl. 21: 1; allotype 61.4000, pl. 21:2.

Lampsilis ventricosa winnebagoensis Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 291, pl. 94, figs. 1–4 (Winnebago Lake, near Oshkosh [Winnebago Co.], Wisconsin; holotype MZUM 209219).

Lampsilis ventricosa perglobosa Baker 1928, Bull. Wisconsin Geol. Nat. Hist. Survey, no. 70(2), p. 285, pl. 93, figs. 1–4 (Lake Pepin, near Lake City [Wabasha Co.], Wisconsin; holotype MZUM 209195).

Lampsilis ovata (Say). Ortmann, 1919, Mem. Carnegie Mus., 8: 297, pl. 17, figs. 8, 9; pl. 18, figs. 1–3.

Lampsilis ovata ventricosa (Barnes). Ortmann, 1919, Mem. Carnegie Mus., 8: 301, pl. 18, fig. 4 pl. 19, figs. 1–3. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 55, figs. 47, 48.

Description. Shell usually medium, though reaching 140 mm in length. Outline of male elliptical or subelliptical, of female subovate, rather short and high. Valves somewhat to considerably inflated, thin when young, becoming thick with age, inequilateral. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin slightly

curved. Dorsal margin short and straight, terminating in a broad angle or gentle curve with the obliquely descending posterior margin. Hinge ligament prominent, occupying most of the dorsal margin. Posterior ridge variable; it may be rounded and poorly defined, though often becoming distinct toward the umbos, and in some habitats the posterior ridge becomes very sharp toward the umbos. Posterior slope varies from gently convex to almost flat, or even concave toward the umbos. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five rather coarse bars, of which the second and third have a slight tendency to fall into two loops, with a small sinus in the middle, while the first, fourth, and fifth bars are indistinct. Surface of the shell generally smooth except for growth ridges. Periostracum usually light or dark yellowish green to olive brown. Dark green or blackish rays which are straight and continuous, finer or broader, often cover the entire surface or only part of it, but some rays are almost always present. On the posterior slope the periostracum is less smooth and usually darker.

Left valve with two slightly compressed pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, located directly under the umbos, both teeth quite chunky. Hinge line rounded with a narrow interdentum under the umbos; two short lateral teeth. Right valve with two opposing pseudocardinals, the anterior one low and laminate, the other higher, quite chunky, and serrated; one lateral tooth, sharply truncated behind. Beak cavities moderately deep, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre silvery or bluish white, sometimes suffused with pink or purple.

Length mm	Height mm	Width mm	
115	78	56	Potomac River, Hancock, Washington Co., Maryland. Female.
111	73	47	South Branch, Potomac River, South Branch, Hampshire Co., West Virginia. Male. Carnegie Mus.
95	60	41	Potomac River, Hancock, Washington Co., Maryland. Lectotype of *L. v. cohongoronta* Ortmann. Male.
87	52	57	As above. Allotype. Female.

Anatomy. Discussed by Ortmann (1911: 351). The glochidia are subelliptical, with a straight line hinge, without hooks, and measure 0.25 mm in length and 0.29 mm in height. Coker, et al. (1921: 153) report the following fish as hosts: bluegill, *Lepomis macrochirus* Rafinesque; white crappie, *Pomoxis annularis* Rafinesque; largemouth bass, *Micropterus salmoides* (Lacépède); smallmouth bass, *M. dolomieui dolomieui* Lacépède; yellow perch, *Perca flavescens* (Mitchill); and yellow pikeperch, *Stizostedion vitreum* (Mitchill).

Breeding season. According to Ortmann (1919: 298, 303, 308) this species is bradytictic.

Habitat. Lives in rivers and creeks on gravel, sand, or even mud bottoms; also occurs in lakes.

Remarks. Lampsilis ovata (Say) is a species of the Interior Basin and St. Lawrence River system which was accidently introduced into the Shenandoah River in 1889 and in other parts of the Potomac River system in 1894, while in the larval stage, on species of bass and other fishes that were transplanted at those times from the west. On the Atlantic Slope *ovata* can be confused only with *Lampsilis cariosa* (Say), with which it is now found in the lower Potomac River system. *L. ovata* generally has a sharper posterior ridge, especially near the umbos, tends to be inflated, has a dull olivaceous tint to the shell, is inclined to be rayed over the entire surface, and has rather heavy chunky

pseudocardinals. *L. cariosa* always has a poorly defined posterior ridge, is not much inflated, usually has a distinctive bright waxy yellow glossy periostracum. Rays when present are usually confined to the posterior slope, and the pseudocardinals are less chunky than those of *ovata*.

The present synonymy of *ovata* may not be the last word spoken on the subject (the author is not yet prepared to comment on the validity of *Unio satur* Lea, which is found in the Western Gulf Coastal region), but it is an attempt to use modern systematic concepts. Ortmann (1919: 298, 303) clearly states that *L. ovata* occurs in large rivers and gradually gives way to *ovata ventricosa* in smaller rivers and streams, that numerous intergrades occur in intermediate areas and, further, that this is a general phenomenon and occurs in widely separated streams. Van der Schalie (1938: 70) discusses a similar change from *ovata ventricosa*, the river form, to the *ovata canadensis*, the lake form, which also intergrade. Goodrich and van der Schalie (1944: 315) again note that, "as one progresses into the headwaters the sharp posterior ridge of the true *ovata* is seen to round off and we pass gradually to the more common form of the species in Indiana, known as *Lampsilis ovata ventricosa* (Barnes)." Cvancara's (1963) work appears to indicate that *ovata* and *ventricosa* are ecophenotypes.

Ortmann (1912: 53) proposed *cohongoronta* as a variety of *Lampsilis ventricosa*, "on account of the small size, the shorter and higher outline, and somewhat more distinct posterior ridge." He found no difference in the anatomy or glochidia from *L. ventricosa*.

When Ortmann wrote in 1912, *Lampsilis ovata* was found on the Atlantic Slope only in the Great Allegheny Valley, an area from which *cariosa* has never been reported. Since that time *ovata* has spread throughout the Potomac River, having reached Great Falls, Maryland, by 1915 (Marshall, 1917: 40). Writing again, Marshall (1930: 19) indicated that *cariosa* was being replaced by *ovata*. This is confirmed by collections made in the Potomac River in 1965 by S. L. H. Fuller.

Range. Interior Basin: Mississippi and Ohio drainages. St. Lawrence drainage from Lake Superior to the Ottawa River and Lake Champlain. Hudson Bay drainage. Northern Atlantic Slope: restricted to the Potomac River system, Maryland (introduced).

Specimens Examined

Potomac River System

Potomac River Drainage. *West Virginia:* South Branch, Potomac River, Romney (Carnegie Mus.); South Branch, Potomac River, South Branch [Depot = French Station] (Carnegie Mus.); *both* Hampshire Co. Cacapon River, 1 mi. above confluence with Potomac River, Morgan Co. (USNM). *Maryland:* Potomac River, Hancock, Washington Co. (Carnegie Mus.). *Virginia:* Shenandoah River, Harpers Ferry, Jefferson Co. (Carnegie Mus.). *Maryland:* Potomac River, Paton Island, 0.75 mi. W Point of Rocks, Frederick Co. Potomac River, 2.5 mi. WSW Dickerson; Potomac River, Harrison Island, 5 mi. above Great Falls (USNM); Potomac River, Great Falls (USNM); Chesapeake and Ohio Canal, Great Falls (USNM); *all* Montgomery Co.

Lampsilis (Lampsilis) ochracea (Say)
Plate 21: 4, 5

Mytilus fluviatilis Gmelin 1791, Systema Naturae, ed. 13, 1, pl. 6, p. 3359 (Europae, aquis dulcibus [erroneous], type [probably based on Lister's figure only]) refers to: Lister, 1685, Synopsis Methodicae Conchyliorum, pl. 157, fig. 12 (Virginia; figured specimen Oxford Univ. Mus. [probably lost] *teste* Dance, 1966, Shell Collecting, p. 292). Conrad (1836, Monography Unionidae, no. 4, p. 37) considered Lister's figure to represent *Lampsilis ochracea* (Say), but the figure is sufficiently ambiguous to have subsequently allowed Isaac Lea to claim successfully, for over fifty years, that *M. fluviatilis* Gmelin was *Anodonta cataracta*

Say. Since Lister makes no reference to dentition or lack of it, his figure cannot be positively identified. Gmelin's name is certainly a *nomen dubium*.

Unio ochraceus Say 1817, Nicholson's Encyclopedia, 2 [no pagination], pl. 3 fig. 8 (Delaware and Schuylkill Rivers; type ANSP [lost]). The type locality was restricted to Schuylkill River, near Philadelphia, Pennsylvania, and a neotype MCZ 178838 was selected by Johnson, 1947, Occ. Papers on Moll., 1: 153, pl. 20, fig. 2.

Lampsilis rosea Rafinesque 1820, Ann. Gén. des Sci. Physiques (Bruxelles), 5: 229 (Hudson River [New York]; type not in ANSP [lost]).

Unio rosaceus Conrad 1849, Proc. Acad. Nat. Sci. Phila., 4: 153 (Savannah River, Georgia, J. H. Couper [loaned]). Conrad, 1850, Jour. Acad. Nat. Sci. Phila., ser. 2, 1: 275, pl. 37, fig. 5; figured holotype MCZ 178779, purchased from J. H. Couper.

Lampsilis ochracea (Say), Simpson, 1914, Cat. Naiades, 1: 49. Ortmann, 1919, Mem. Carnegie Mus., 8: 318, pl. 20, figs. 6, 7. Johnson, 1947, Occ. Papers on Moll., 1: 150, pl. 20, figs. 1–2. Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem., no. 367, p. 57, figs. 55, 56. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 30, pl. 4, figs. 3, 4.

Description. Shell usually small, seldom exceeding 70 mm in length. Outline of male elliptical and somewhat elongate; of female subovate, rather short and high. Valves inequilateral, subinflated, rather thin, though strong, sometimes translucent. Anterior end regularly rounded; posterior end more broadly rounded and somewhat pointed in the male, truncated in the female. Ventral margin usually straight or slightly curved, sometimes concave in females. Dorsal margin straight or slightly curved, terminating in a broad angle with the obliquely descending posterior margin. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rounded and generally poorly defined. Posterior slope slightly convex, usually with a few faint ridges and wrinkles. Umbos moderately swollen, slightly raised above the hinge line, located somewhat anterior to the middle of the shell, their sculpture consisting of four or five wavy recurved ridges. Surface of the shell generally smooth in the region of the disk, becoming roughened with periostracum posteriorly. Periostracum usually subshiny, brownish olive, brownish, greenish yellow, reddish yellow, or yellow. Dull, rather fine, greenish rays sometimes found over the entire surface of the shell, especially in immatures.

Left valve with two compressed, serrated pseudocardinal teeth, one in front of the other, the anterior one somewhat triangular, the hinder one lower, inclined to be vestigial. Hinge line rather long and narrow before two short, curved lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a deep narrow pit, the more anterior tooth inclined to be vestigial; one lateral tooth. Beak cavities shallow, with deep dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line not very distinct. Nacre white, bluish white, or pinkish, usually iridescent.

Length mm	Height mm	Width mm	
73	44	27	Savannah River, Georgia. Holotype of *U. rosaceus* Conrad. Male.
50	31	19	Schuylkill River, near Philadelphia, Pennsylvania. Neotype. Male.
54	38	24	Halfway Pond, Plymouth, Plymouth Co., Massachusetts. Female.

Anatomy. Figured by Lea (1838: pl. 15, fig. 44) and described (1863: 455) also by Reardon (1929: 1, pl. 1, figs. 1–10). The host fish is unknown, but since *ochracea* is generally restricted to the lower regions of streams or bodies of water directly connected with the ocean, it may, like *Anodonta implicata* Say, parasitize a migratory fish.

Breeding season. Lea (1863: 455) found this species gravid in the autumn. I found gravid females on May 3, 1943 in Plymouth, Massachusetts. It is probably bradytictic.

Habitat. Lives in sand or mud in ponds, canals, and the lower portions of rivers to-

ward the tidal region in areas where the current is not strong.

Remarks. In the Atlantic Slope region, *Lampsilis ochracea* (Say) has been confused with *L. cariosa* (Say), but *ochracea* has a thinner, smaller shell and, unlike *cariosa* which is rarely rayed, *ochracea* is often rayed over the entire surface. It has a rougher, duller, more greenish periostracum. The hinges are quite different. The pseudocardinals of *cariosa* are pyramidal and an interdentum is present, but in *ochracea* the pseudocardinals are lamellate, almost parallel to the hinge line, and there is no interdentum.

Lampsilis ochracea may also be mistaken for immature *Lampsilis splendida* (Lea), but only in that the shells of both may be rayed over the entire surface. The rays of *ochracea* are finer, and the shell is more yellowish, whereas that of *splendida* is more brownish, less delicate, and more inflated.

Simpson (1914: 49) gives the range of this species as from "New England to the Ogeechee River, Georgia." The specimen in the United States National Museum on which he based the Ogeechee record from Le Conte appears to be a young *cariosa*. Unfortunately, in none of the major museums are there any precisely labeled specimens of *ochracea* from the Savannah River, the apparent southern limit of its distribution. Conrad (1836: 37) reports *ochracea* as occurring in, "most of the tide waters north of Savannah River."

Range. Atlantic Slope: Savannah River system, Georgia, north to River Herbert, Nova Scotia (Athearn and Clarke, 1962: 30).

Specimens Examined

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River (MCZ and USNM).

Waccamaw River System

Waccamaw River Drainage. *North Carolina*: Lake Waccamaw, [town of] Lake Waccamaw; drainage canal, beside Lake Waccamaw, 1 mi. NNW Dupree Landing; *both* Columbus Co. *South Carolina:* Waccamaw River, Wachasaw Landing, 2 mi. W Murrells Inlet, Georgetown Co.

Pamlico River System

Tar River Drainage. *North Carolina*: Tar River, Old Sparta, 3.5 mi. W Pinetops, Edgecombe Co. Tar River, Bruce, 9 mi. NW Greenville, Pitt Co.

Roanoke River System

Roanoke River Drainage. *North Carolina*: Roanoke River, Weldon, Halifax Co. (USNM).

James River System

Appomattox River Drainage. *Virginia*: Petersburg, Dinwiddie Co. (USMN).

James River Drainage. *Virginia*: James River (MCZ and USNM).

York River System

Mattaponi River Drainage. *Virginia*: Mantapike Creek, Mantapike, King and Queen Co. (USNM).

York River Drainage. *Virginia*: York River (MZUM).

Potomac River System

Potomac River Drainage. *Virginia*: Potomac River, Great Falls, Fairfax Co. *District of Columbia*: Potomac River. Anacostia River. *Virginia:* Canal, Alexandria (MZUM); Little Hunting Creek, near Mt. Vernon (MZUM); *both* Fairfax Co.

Lampsilis (Lampsilis) radiata radiata (Gmelin) Plate 22: 1–3

Mya radiata Gmelin 1791, Systema Naturae, ed. 13, 1, pt. 6, p. 3220 (Malabariae [erroneous]) refers to: Martini and Chemnitz, 1782, Conch. Cabinet, 6, pl. 2, fig. 7 ([source of Gmelin's locality]; figured specimen Spengler colln. Copenhagen, [lost] *teste* Haas, 1913, Vidensk. Meddr. Dansk naturh. Foren. [Copenhagen], 65: 59); also Lister, 1685, Synopsis Methodicae Conchyliorum, pl. 152, fig. 7 (Virginia; figured specimen, Oxford Univ. Mus. [probably lost]

teste, Dance, 1966, Shell Collecting, p. 292). The figure in Martini and Chemnitz is here selected as the type figure, and the type locality, following Lister and Simpson (1914, Cat. Naiades, 1: 64), is here restricted to Potomac River, District of Columbia (approximately opposite, Fairfax Co., Virginia).

Unio luteola Lamarck 1819, Hist. Nat. des Animaux sans Vertèbres, 6: 79 (la rivière Susquehana [Susquehanna River, Pennsylvania] et celle Mohancks [Mohawk River, New York]; measured holotype Paris Museum, figured by Wheeler, 1963, Nautilus, 77: 58, pl. on p. 59, figs. 1–2. Refigured by Johnson, 1969, Nautilus, 83: 54, fig. 11, the type locality was restricted to the Susquehanna River, Columbia, York Co., Pennsylvania).

Unio lineata 'Valenciennes' Bory de St. Vincent 1827, Encyclopédie Méthodique, 2 of atlas, explanation of pls., p. 151, pl. 248, fig. 5 (no locality, type [presumed lost]). [Named from figure published in 1797.]

Unio tenebrosus Conrad 1834, New Fresh Water Shells United States, p. 42, pl. 7, fig. 1 (Rappahannock [*sic*] River, near Falmouth, Stafford Co., Virginia; type presumably in Poulson colln., ANSP [lost]).

Unio melinus Conrad 1838, Monography Unionidae, no. 11, p. 101, pl. 56, fig. 1 (Salina Lake [Onondaga Co.], New York; type, not in ANSP, presumed lost).

Unio boydianus Lea 1840, Proc. Amer. Philos. Soc., p. 286 (Oak Orchard Creek, Orleans Co., New York). Lea, 1843, Trans. Amer. Philos. Soc., 8: 216, pl. 16, fig. 32; figured holotype USNM 86126). Lea, 1942, Obs. Unio, 3: 54.

Unio rosaceus De Kay 1843, Zool. New York, Moll., pt. 5, p. 192, pl. 39, figs. 355, 356; pl. 40, fig. 357 (Seneca Lake [North Western], New York; lectotype, here selected, USNM 678303, formerly New York State Cabinet 391, specimen figured on pl. 39, fig. 356).

Mya oblongata Wood 1856, Index Testaceologicus, ed. Hanley, p. 199, Supplement, pl. 1, fig. 2 (North America, type [lost]).

Unio elongata S. G. Goodrich 1859, Illustrated Natural History, 2: 523, text fig. (No locality, type [probably not saved].)

Unio obliquiradiatus Reeve 1856, Conch. Iconica, 16, *Unio*, pl. 29, figs. 151 (Hab ?, Mus. Cuming, type [not in BMNH, lost]).

Unio conspicuus Lea 1872, Proc. Acad. Nat. Sci. Phila., 24: 156 (Yadkin River, Salisbury, [Rowan Co.], North Carolina). Lea, 1874, Jour. Acad. Nat. Sci. Phila., ser. 2, 8: 34, pl. 11, fig. 31; figured holotype USNM 85056. Lea, 1874, Obs. Unio, 13: 38.

Unio virginiana Simpson, 1900, Proc. United States Natl. Mus., 22: 536, *non* Lamarck 1819. Lamarck's type examined and identified as *Elliptio complanatus* Solander [*sic*] *teste* Johnson, 1953, Nautilus, 66: 95.

Lampsilis radiata (Gmelin). Simpson, 1914, Cat. Naiades, 1: 64. Ortmann, 1919, Mem. Carnegie Mus., 8: 292, pl. 17, figs. 6, 7.

Lampsilis radiata oneidensis Baker 1916, Nautilus, 30: 74, pl. 2 (Oneida Lake, Central New York; syntypes, New York State College of Forestry, Syracuse, New York; ANSP 114854; MZUM).

Unio virginea Frierson 1927, Check List North American Naiades, p. 72, error for *Unio virginiana* Lamarck 1819, *non* Lamarck.

Lampsilis radiata radiata (Gmelin). Clarke and Berg, 1959, Cornell Univ. Exp. Sta. Mem. no. 367, p. 58, fig. 53. Athearn and Clarke, 1962, Natl. Mus. Canada, Bull. no. 183, p. 31, pl. 4, figs. 5, 6.

Lampsilis radiata var. *conspicua* (Lea). Simpson, 1914, Cat. Naiades, 1: 66.

Description. Shell large, often reaching over 100 mm in length. Outline subelliptical or subovate, moderately elongated, distinctly over one and a half times as long as high. Valves generally subinflated, though occasionally quite inflated, and solid. Anterior end regularly rounded; posterior end more broadly rounded, and in females often somewhat expanded in the postbasal region, though not uniformly so. Ventral margin generally regularly curved, sometimes straight, roughly parallel to the almost straight dorsal margin which forms a blunt angle with the posterior margin in immatures, and becomes almost imperceptible with age. Hinge ligament prominent. Posterior ridge feeble or wanting. Posterior slope broad and undistinguished. Umbos rather sharp, but not full or high, their sculpture consisting of six to ten double-looped bars, with a distinct re-entering angle in the middle. The posterior loop is slightly angular and indistinct on the posterior slope. Surface roughened by close concentric wrinkles of periostracum, generally yellowish or brownish green, with dark greenish or blackish rays, both narrow and wide, over the entire surface.

Left valve with two stumpy pseudocardinal teeth, both rather triangular and crenulate. No interdentum. Two long, slightly curved lateral teeth. Right valve

with one rather high, triangular pseudocardinal, and a vestigial one before it; one lateral tooth. Beak cavities very shallow, with a few dorsal muscle scars. Anterior and posterior adductor muscle scars and pallial line all distinct. Nacre generally white, bluish white, sometimes tinted with pink or salmon, sometimes quite pink or salmon.

Length mm	Height mm	Width mm	
138	86	46	Lake Michie, 12 mi. NNE Durham, Durham Co., North Carolina. Male.
112	64	39	Yadkin River, near Salisbury, Rowan Co., North Carolina. Holotype of *U. conspicuus* Lea. Male.
99	52	29	Susquehanna River, Columbia, York Co., Pennsylvania. Male.
84	49	27	Potomac River, Washington, District of Columbia. Male.
62	39	20	As above. Female.

Anatomy. Figured by Lea (1838, pl. 15, figs. 48, 49). According to Ortmann (1911: 349) the anatomy of *L. radiata radiata* agrees "in all essential respects" with that of *L. r. siliquoidea* (Barnes). The glochidia are suboval, without hooks, and measure 0.22 to 0.23 mm in length and 0.27 to 0.28 mm in height. The host fish is unknown.

Breeding season. Ortmann (1919: 293) indicates that the breeding season begins in August and ends the following August.

Habitat. Lives in rivers and lakes of all sizes, usually in gravel or sand, occasionally in mud. Prefers tidewaters, but ascends some of the larger rivers, such as the Susquehanna River, Pennsylvania, and the Hudson River, New York, for a considerable distance.

Remarks. In the Southern Atlantic Slope region *Lampsilis radiata radiata* (Gmelin) is replaced by *Lampsilis splendida* (Lea) below the Pedee River system. But the two species do not much resemble one another, as *splendida* has a sharp posterior ridge and *r. radiata* does not. See: *Remarks* under *splendida* on p. 394. *Lampsilis r. radiata*, an Atlantic Slope species, most closely resembles *Lampsilis radiata siliquoidea* (Barnes) which is found throughout the Interior Basin. Clarke and Berg (1959: 58–62, 68–70) have shown that in the Lower St. Lawrence drainage of New York where these two otherwise quite distinct "species" commingle, they intergrade completely.

Typically, *L. r. radiata* is easily distinguished from *L. r. siliquoidea.* The former is more compressed; the difference between the male and female shell is much less marked; the periostracum is always rough and not shiny like that of *siliquoidea.* It has broader rays and often has a reddish or salmon nacre. In *siliquoidea* the nacre is always bluish white.

Ortmann (1919: 296) *suggested* for the type locality of *r. radiata* Saratoga Lake in New York, "should there not be any earlier record," and was probably unaware that Simpson (1914, 1: 65) had already selected Virginia as the type locality.

Ortmann and Walker (1922: 61) have shown that *Unio luteolus* Lamarck is not recognizable on the basis of the original description. Wheeler (1963: 58) has tried to resurrect this name on the basis of the identification of the type. Lamarck originally gave two localities, the Susquehanna and the Mohawk rivers. The former has only *L. r. radiata*, and the latter, which is now in the region of hybridization, probably did not have *L. r. siliquoidea* in it before the completion of the Erie Canal, some years after Lamarck's specimen was collected. Therefore, to avoid further confusion the type locality was restricted to the Susquehanna. See: synonymy above.

Simpson (1914, 1: 66) treats *Unio conspicuus* Lea as a variety of *Lampsilis r. radiata,* stating that "there are intermediates, which seem to fully connect the two." I am in agreement with him. The main difference in the southern specimens seems to be a general tendency to grow large more consistently than elsewhere. There

does seem to be a hiatus for this species between the Neuse River, North Carolina, and the Potomac River, Virginia. Ortmann (1919: 296) calls attention to the fact that while this species is abundant in the tidewater region of the Potomac River, it does not go up the river into the mountains west of the Blue Ridge, and is rare or absent on the Piedmont Plateau.

Range. Southern Atlantic Slope: discontinuous, Pedee River system, South Carolina, Cape Fear and Neuse river systems, *both* North Carolina. Northern Atlantic Slope: Potomac River, Maryland, north to the St. Lawrence River system, westward to Lake Ontario.

Specimens Examined

Pedee River System

Yadkin River Drainage. *North Carolina:* [Yadkin River], Salem, Forsyth Co. (MZUM). Yadkin River, near Salisbury, Rowan Co. (MZUM).

Cape Fear River System

Cape Fear River Drainage. *North Carolina:* Greenfield Pond, Wilmington, New Hanover Co. (USNM).

Neuse River System

Neuse River Drainage. *North Carolina*: Lake Michie [an impoundment on Flat River], 12 mi. NNE Durham Center, Durham Co. (75).

Potomac River System

Potomac River Drainage. *Virginia*: Potomac River, Great Falls, Fairfax Co. *District of Columbia:* Potomac River. *Virginia:* Mount Vernon, Fairfax Co.

Lampsilis (Lampsilis) splendida (Lea)
Plate 22: 4, 5

Unio splendidus Lea 1838, Trans. Amer. Philos. Soc., 6: 70, pl. 19, fig. 61 (Altamaha River, near Darien [McIntosh Co.]; Altamaha [River], Liberty [now Long] Co.; *both* Georgia; figured holotype USNM 84893). Lea, 1838, Obs. Unio, 2: 70.

Unio regularis Sowerby 1866, Conch. Iconica, 16, *Unio*, pl. 34, fig. 181, *non* Lea 1841.

Lampsilis splendida Lea. Simpson, 1914, Cat. Naiades, 1: 50.

Description. Shell large, often exceeding 110 mm in length. Outline obovate and elongated, the female proportionally higher than the male. Valves considerably inflated, subsolid. Anterior end rounded; posterior end of the male broader and very bluntly pointed; the female even more broadly rounded. Ventral margin usually slightly curved, or slightly arcuate in males when they are swollen behind the middle of the base. Dorsal margin straight, sometimes forming a distinct angle with the obliquely descending posterior margin or merging gradually into it. Hinge ligament prominent, running under the umbos and appearing anteriorly. Posterior ridge rather sharp, generally with a second ridge above it. Posterior slope considerably wrinkled. Umbos very high and full, their sculpture consisting of a number of strong, nearly straight bars. Surface of the disk sometimes smooth, but the periostracum is usually concentrically wrinkled, especially posteriorly and toward the margins. Periostracum yellowish green to brownish with the entire surface covered with numerous wide and narrow green rays. Old shells sometimes dark brown with the rays obscured.

Left valve with two compressed pseudocardinal teeth slightly anterior of the umbos, one in front of the other, the anterior one somewhat triangular; the hinder one considerably lower. Hinge line very narrow, before two short, curved, lateral teeth. Right valve with two triangular, narrow, parallel pseudocardinals separated by a deep narrow pit, the more anterior tooth inclined to be vestigial; the hinder tooth inclined to be chunky in old specimens. One rather high lateral tooth present. Beak cavities deep and wide, with dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line distinct. Nacre white, orange,

violet, sometimes bluish, but more inclined to be pinkish and iridescent.

Length mm	Height mm	Width mm	
112	68	54	Ocmulgee River, 1 mi. S Lumber City, Telfair Co., Georgia. Female.
113	62	59	As above. Male.
73	46	36	As above. Female.
70	42	33	As above. Male.

Anatomy. Discussed by Lea (1863: 414).

Habitat. Usually lives in the swift waters of large rivers on sand bars and gravelly bottoms, but also lives in lakes.

Remarks. Lampsilis splendida (Lea) does not closely resemble any of the *Lampsilis* in either the Apalachicolan or Atlantic Slope regions. It replaces *Lampsilis radiata radiata* (Gmelin) in the Atlantic Slope region below the Pedee River system, South Carolina. *L. splendida* resembles *L. r. radiata* in its tendency to have rays which cover the entire shell, but *r. radiata* does not have a posterior ridge, while *splendida* often has quite an angular one. In *splendida* the shell of the female is proportionally higher than that of the male and more blunt behind, while in *radiata* the main difference in the shell is a tendency for the female to be expanded in the postbasal region. Young specimens of *L. ochracea* (Say) can be confused with *splendida* when the former are rayed over the entire surface, but the rays of *splendida* are narrow and wide, while those of *ochracea* are rather uniformly narrow. *L. splendida* has a much heavier shell and even in immatures the shell is heavier than the shells of *ochracea* of corresponding size.

Range. Southern Atlantic Slope: Altamaha River system, Georgia, north to the Cooper-Santee River system, South Carolina.

Specimens Examined

Altamaha River System

Ocmulgee River Drainage. *Georgia*: Limestone Creek, Brumbys Mill, 4 mi. NE Hawkinsville; Ocmulgee River, Hawkinsville; Mosquito Creek, 8 mi. SE Hawkinsville; *all* Pulaski Co. Dicksons Creek, 10 mi. NE Fitzgerald; House Creek, Bowens Mill, 9 mi. N Fitzgerald; *both* Ben Hill Co. Ocmulgee River, Jacksonville; Ocmulgee River, 1 mi. S Lumber City; *both* Telfair Co.

Oconee River Drainage. *Georgia*: Oconee River, 2.5 mi. N Glenwood, Wheeler Co.

Altamaha River Drainage. *Georgia*: Altamaha River, 7 mi. N Glenwood, Wheeler Co. Altamaha River, 10 mi. NE Surrency, Appling Co. Altamaha River, "Riverside Park," 4 mi. N Jesup, Wayne Co. Altamaha River, 3 mi. NW Everett City, Glynn Co. Altamaha River, Fort Barrington; Altamaha River, Hopeton, near Darien; *both* McIntosh Co.

Ogeechee River System

Ogeechee River Drainage. *Georgia*: Reported by Simpson (1914: 51) but the specimens were not located in the USNM.

Savannah River System

Savannah River Drainage. *Georgia*: Savannah River, 0.75 mi. SE Augusta, Richmond Co. *South Carolina:* Savannah River, 2 mi. SW Millettville; Savannah River, Johnsons Landing, 10 mi. W Allendale; Savannah River, Kingjaw Point, 10 mi. WSW Allendale; *all* Allendale Co. (*all* ANSP). *Georgia:* Savannah River, 7.5 mi. NE Shell Bluff; Savannah River, 6 mi. NE Girard; *both* Burke Co.

Cooper-Santee River System

Wateree River Drainage. *South Carolina:* Wateree River, 2.5 mi. W Camden, Kershaw Co.

Santee River Drainage. *South Carolina*: Lake Moultrie, Cross; Santee River, 1 mi. N Moncks Corner; Bunnon Lake [not located], near Alvin (ANSP and USNM); *all* Berkeley Co.

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INDEX TO RELEVANT TAXA

Principal references in boldface type.

abbevillensis Lea, *Unio*, 315
aberrans Lea, *Unio*, 317
ablatus Lea, *Unio*, 327
Aeglia Swainson, 382
aequatus Lea, *Unio*, 326
alabamensis Lea, *Margaritana*, 366
Alasmidonta Say, 346, 348
Alasminota Ortmann, 343
Alasmodonta Say, 348
amplus Lea, *Unio*, 318
angulata (Lea), *Gonidea*, 265
angustatus Lea, *Unio*, 333
annulatus Sowerby, *Anodon*, 367
Anodonta Lamarck, 356
anodontoides (Lea), *Lampsilis*, 271
anthonyi Lea, *Unio*, 312
Anodontinae (Swainson) Ortmann, 343
aquilus Lea, *Unio*, 326
arctata (Conrad), *Elliptio* (*Elliptio*), 271, 274, 276, **331**
arctatus Conrad, *Unio*, 331
arcula (Lea), *Alasmidonta* (*Alasmidonta*), 274, 278, **352**
arcula Lea, *Margaritana*, 352
arcolatus Swainson, *Anodon*, 367
arkansasensis Lea, *Anodonta*, 367
atropurpureum Rafinesque, *Alasmidon*, 353
attentuata Rafinesque, *Obliquaria*, 380
attenuatus Lea, *Unio*, 380
aurata Rafinesque, *Unio*, 315
australis Simpson, *Lampsilis*, 272
averellii B. H. Wright, *Unio*, 373

baldwinensis Lea, *Unio*, 316
barrattii Lea, *Unio*, 326
basalis Lea, *Unio*, 318
beaverensis Lea, *Unio*, 318
binominatus Simpson, *Lampsilis*, 273, 385
bisselianus Lea, *Unio*, 340
blandingianus Lea, *Unio*, 339
boydianus Lea, *Unio*, 391
boykiniana (Lea), *Amblema*, 271
brimleyi S. H. Wright, *Unio*, 301
buddianus Lea, *Unio*, 339
Bullella Simpson, 348
burkei Walker, *Quincuncina*, 273
burkensis Lea, *Unio*, 316
burtchianus S. H. Wright, *Unio*, 327
buxeus Lea, *Unio*, 308

calceola (Lea), *Alasmidonta*, 279, 349
camptodon Say, *Unio*, 339
canadensis Lea, *Unio*, 386
Canthyria Swainson, 303
cardium Rafinesque, *Lampsilis*, 386
carinifera Lamarck, *Unio*, 314

cariosa (Say), *Lampsilis* (*Lampsilis*), 274, 275, 276, 278, 279, **382**
cariosus Say, *Unio*, 382
Carunculina Baker, 369
castus Lea, *Unio*, 301
cataracta Say, *Anodonta* (*Pyganodon*) *cataracta*, 272, 274, 276, 278, 279, 286, **356**
catawbensis Lea, *Unio*, 315
charlottensis Lea, *Unio*, 344
chathamensis Lea, *Unio*, 317
chipolaensis (Walker), *Elliptio*, 273
choctawensis Athearn, *Villosa*, 273
cicur Lea, *Unio*, 340
cirratus Lea, *Unio*, 319
cistelliformis Lea, *Unio*, 317
claibornensis (Lea), *Lampsilis*, 271, 382
coarctata Lamarck, *Unio*, 314
cohongoronata Ortmann, *Lampsilis ventricosa* 386
collina Conrad, *Pleurobema* (*Lexingtonia*), 274, 277, **300**
collinus Conrad, *Unio*, 300
columbensis Lea, *Unio*, 340
complanata (Lightfoot), *Elliptio* (*Elliptio*), 272, 274, 278, 279, 286, **314**
complanata (Lightfoot), *Mya*, 314
compressa (Lea), *Lasmigona*, 280, 343, 345
compressa Lea, *Symphynota*, 343
concavus Lea, *Unio*, 376
confertus Lea, *Unio*, 325, 329
congaraea (Lea), *Elliptio* (*Elliptio*), 274, 276, 277, 278, **308**
congaraeus Lea, *Unio*, 308
conica Rafinesque, *Pleurobema*, 299
conspicuus Lea, *Unio*, 391, 394
constricta (Conrad), *Villosa*, 274, 277, 278, 280, 285, **378**
constrictus Conrad, *Unio lienosus*, 378
contiguus Lea, *Unio*, 376
contractus Lea, *Unio*, 316
contrarius Conrad, *Unio*, 382
corneus Lea, *Unio*, 319
corrugata DeKay, *Alasmidon*, 354
Corunculina Simpson, 370
coruscus Gould, *Unio*, 326
corvus Lea, *Unio*, 308
costata Rafinesque, *Alasmidonta*, 243
couperiana Lea, *Anodonta* (Utterbackia), 272, 274, 275, 276, **365**
cowperiana Lea, *Anodonta*, 365
crassidens (Lamarck), *Elliptio* (*Elliptio*) *crassidens*, 267, 271, 277, **305**
crassidens var. b. Lamarck, *Unio*, 305
crocatus Lea, *Unio*, 382
cuneata Rafinesque, *Pleurobema*, 299
cuneatus Barnes, *Unio*, 305
Cunicula Swainson, 305
cuprea Rafinesque, *Obliquaria*, 333
curatus Lea, *Unio*, 317
curvatus Lea, *Unio*, 318
cuspidatus Lea, *Unio*, 327
cuvierianus Lea, *Unio*, 315
cygneus Linnaeus, *Mytilus*, 356, 362
cylindraceus Frierson, *Elliptio*, 327

danielsii B. H. Wright, *Unio*, 305
dariensis Lea, *Anodonta*, 357
dariensis (Lea), *Elliptio* (*Elliptio*), 274, 277, 278, **310**
dariensis Lea, *Unio*, 310
datus, Lea, *Unio*, 318
declivis Say, *Unio*, 339
decoratus Lea, *Unio*, 344
Decurambis Rafinesque, 353
delumbis Conrad, *Unio*, 375
delumbis (Conrad), *Villosa*, 274, 276, 277, **375**
diazensis S. H. Wright, *Unio*, 327
differtus Lea, *Unio*, 318
dilatata (Rafinesque), *Elliptio*, 270, 279, 280, 305
dilatatus Rafinesque, *Unio*, 305
discus Sowerby, *Unio*, 305
dispalans B. H. Wright, *Unio*, 327
dispar Lea, *Unio*, 373
dissimilis Lea, *Unio*, 319
dolabraeformis (Lea), *Lampsilis* (*Lampsilis*), 274, 278, **384**
dolabraeformis Lea, *Unio*, 384
dolearis Lea, *Anodonta*, 357
doliaris Lea, *Anodonta*, 357
dooleyensis Lea, *Unio*, 319
dorsatus Lea, *Unio*, 308
downiei (Lea), *Elliptio* (*Elliptio*) *crassidens*, 267, 273, **307**
downiei Lea, *Unio*, 307
dunlapiana Lea, *Anodonta*, 365
duttonianus Lea, *Unio*, 333

edentula Say, *Alasmidonta*, 367
edentulus Say, *Strophitus*, 368
electrinus Reeve, *Unio*, 340
Elliptio Refinesque, 303, 304
elongata Goodrich, *Unio*, 391
emmonsii Lea, *Unio*, 333
errans Lea, *Unio*, 315
escambia Clench and Turner, *Fusconaia*, 272
Euryria Rafinesque, 305
exactus Lea, *Unio*, 316
exacutus Lea, *Unio*, 334
excavatus (Lea), *Lampsilis*, 271, 385
excultus Conrad, *Unio*, 339
excurvata DeKay, *Anodon*, 356
exiguus Lea, *Unio*, 373
extensus Lea, *Unio*, 333

fisherianus Kuester, *Unio*, 280
fisherianus Lea, *Unio*, 333, 334
fisheropsis De Gregorio, *Unio arctior*, 334
floridensis (Lea), *Lampsilis anodontoides*, 270
fluviatilis Gmelin, *Mytilus*, 388
fluviatilis Green, *Unio*, 315

folliculatus Lea, *Unio*, 333
forbesianus Lea, *Unio*, 308
fragilis Lamarck, *Anodonta cataracta*, 266, 279, **357**
fraterna (Lea), *Elliptio (Elliptio)*, 272, 274, 276, 277, **312**
fraternus Lea, *Unio*, 312
fryanus B. H. Wright, *Unio*, 327
fuliginosus Lea, *Unio*, 315
fulvus Lea, *Unio*, 308
fumatus Lea, *Unio*, 316
fusca Baker, *Utterbackia imbecillis*, 363
fuscatus Lea, *Unio*, 326
Fusconaia Rafinesque, 300

gastonensis Lea, *Unio*, 317
geddingsianus Lea, *Unio*, 326
geminus Lea, *Unio*, 315
genthii Lea, *Unio*, 378
genuinus Lea, *Unio*, 376
geometricus Lea, *Unio*, 339
georgina Lamarck, *Unio*, 314
gesnerii Lea, *Anodonta*, 356
gesnerii Lea, *Unio*, 319
gibbesianus Lea, *Unio*, 308
gibbosa Say, *Anodonta (Pyganodon)*, 274, 278, **359**
glabrata Lamarck, *Unio*, 314
glabratus Sowerby, *Unio*, 349
globosa Lea, *Anodonta*, 356
gracilentus Lea, *Unio*, 332
gracilior Lea, *Unio*, 373
grandis Say, *Anodonta*, 271, 279, 360
griffithianus Lea, *Unio*, 315

haddletoni Athearn, *Lampsilis*, 373
hallenbeckii Lea, *Anodonta*, 356, 358
hallenbeckii Lea, *Unio*, 316
hartwrightii B. H. Wright, *Unio*, 310
hazelhurstianus Lea, *Unio*, 333
hebes Lea, *Unio*, 340
hembeli (Conrad), *Margaritifera*, 271
Hemiodon Swainson, 348
henryana Lea, *Anodonta*, 363
hepaticus Lea, *Unio*, 327
heterodon (Lea), *Alasmidonta (Prolasmidonta)*, 274, 279, 281, **347**
heterodon Lea, *Unio*, 346, 347
hians Valenciennes, *Unio*, 349
hopetonensis (Lea), *Elliptio (Elliptio)*, 274, 278, **324**
hopetonensis Lea, *Unio*, 324
horda Gould, *Anodon*, 363
housatonica Linsley, *Anodonta*, 361
humerosus Lea, *Unio*, 318
hyalinus Lea, *Unio*, 344

icterina (Conrad), *Elliptio (Elliptio)*, 272, 274, 276, **325**
icterinus Conrad, *Unio*, 325
imbecilis Say, *Anodonta*, 363
imbecilis Say, *Anodonta* (*Utterbackia*), 271, 274, 276, **362**
implicata Say, *Anodonta*, 360
implicata Say, *Anodonta (Pyganodon)*, 274, 275, 279, **360**
incerta Lea, *Anodonta*, 363
incrassatus Lea, *Unio*, 305
indefinitus Lea, *Unio*, 317
indifinitus Lea, *Unio*, 317
inceptus Lea, *Unio*, 339
infulgens Lea, *Unio*, 319
infurcata (Conrad), *Quincuncina*, 272
infuscus Lea, *Unio*, 318
insolidus Lea, *Unio*, 344
insulsus Lea, *Unio*, 315
inusitatis Lea, *Unio*, 324
invenustus Lea, *Unio*, 319
irwinensis Lea, *Unio*, 318

jamesianus Lea, *Unio*, 340
jayensis Lea, *Elliptio*, 272, 335
jejunus Lea, *Unio*, 315
jewettii Lea, *Unio*, 340
jonesi van der Schalie, *Lampsilis*, 273
Jugosus Simpson, 348

lacustris Lea, *Anodonta*, 356
lacustris Baker, *Strophitus rugosus*, 367
Lampsilinae (Ihering) Ortmann, 369
Lampsilis Rafinesque, 382
lanceolata (Lea), *Elliptio (Elliptio)*, 272, 274, 276, 278, 279, 281, **333**
lanceolatus Lea, *Unio*, 333
lapillus Say, *Unio*, 372
Lasmigona Rafinesque, 343
Lastena Rafinesque, 362
latissima Rafinesque, *Ligumia recta*, 380
latissimus Sowerby, *Unio*, 386
latus Lea, *Unio*, 316
lazarus Lea, *Unio*, 331
lazarus Sowerby, *Unio*, 317
lecontianus Lea, *Unio*, 308
lehmanii S. H. Wright, *Unio*, 305
lenis Conrad, *Unio*, 386
Lexingtonia Ortmann, 300
lienosa (Conrad), *Villosa*, 271, 274, 276, 277, 376
ligatus Lea, *Unio*, 318
Ligumia Swainson, 380
limatulus Conrad, *Unio*, 326
lincata 'Valenciennes' Bory de St. Vincent, *Unio*, 391
lividus Rafinesque, *Unio*, 369
livingstonensis Lea, *Unio*, 327
lucidus Lea, *Unio*, 327
lugubris Lea, *Unio*, 325
lurida Simpson, *Lampsilis ventricosa*, 386
luteola Lamarck, *Unio*, 391
lutcolus Lamarck, *Unio*, 391

macer Lea, *Unio*, 315
maconensis Lea, *Unio*, 333
maineusis Rich, *Unio complanatus*, 319
majusculus De Gregorio, *Unio pullatus*, 319
manubius Gould, *Unio*, 340

margaritifera (Linnaeus), *Margaritifera*, 265, 266, 279, 280
marginata (Say), *Alasmidonta*, 266, 279, 280, 281, 355
marginata Say, *Anodonta*, 356
masoni (Conrad), *Pleurobema (Lexingtonia)*, 274, 277, 278, **301**
masoni Conrad, *Unio*, 301
maywebbae B. H. Wright, *Elliptio*, 327
mccordi Athearn, *Alasmidonta*, 270
mcmichaeli Clench and Turner, *Elliptio*, 312, 313
mecklenbergensis Lea, *Unio*, 317
mediocris Lea, *Unio*, 317
melinus Conrad, *Unio*, 391
merceri Lea, *Unio*, 327
merus Lea, *Unio*, 301
micans Lea, *Unio*, 326
Micromya Agassiz, 371
modioliformis Lea, *Unio*, 373
Monodonta Say, 348
monrocnsis Lea, *Unio*, 310
moussonianus Lea, *Unio*, 308
Mutelacea, 264
mytiloides Rafinesque, *Pleurobema*, 299
mytiloides Swainson, *Unio*, 348, 349

nasuta (Say), *Ligumia*, 274, 275, 279, 281, **380**
nasutus Say, *Unio*, 380
nasutilus Lea, *Unio*, 334
nasutulus Lea, *Unio*, 334
naviculoides Lea, *Unio*, 333
neglecta (Lea), *Lasmigona*, 343
neisleri (Lea), *Amblema*, 273
neusensis Lea, *Unio*, 316
newtonensis Lea, *Anodonta*, 361
nigella (Lea), *Elliptio*, 273
nigra Rafinesque, *Unio*, 305
nigrinus Lea, *Unio*, 373
nolani B. H. Wright, *Unio*, 327
northamptonensis Lea, *Unio*, 317
nubilus Lea, *Unio*, 318

obesus Lea, *Unio*, 339
obfuscus Lea, *Unio*, 373
oblatus Lea, *Unio*, 327
obliquiradiatus Sowerby, *Unio*, 391
oblongata Wood, *Unio*, 391
oblongus Lea, *Unio*, 391
obnubilis Lea, *Unio*, 326, 329
occidens Lea, *Unio*, 386
occultus Lea, *Unio*, 326
ochracea (Say), *Lampsilis (Lampsilis)*, 274, 275, 276, 279, **388**
ochraceus Say, *Unio*, 389
ocmulgeensis Lea, *Unio*, 327
ogeecheensis Conrad, *Unio*, 375
ohiensis Rafinesque, *Anodonta (Lastena)*, 362
oneidensis Baker, *Lampsilis radiata*, 391
opacus Lea, *Unio*, 326
oratus Conrad, *Unio*, 382
ovata (Say), *Lampsilis (Lampsilis)*, 274, 279, **386**
ovata Valenciennes, *Unio*, 382
ovatus Frierson, *Strophitus undulatus*, 367
ovatus Say, *Unio*, 382, 386

pachyodon Pilsbry, *Elliptio*, 306
palliatus 'Ravenel' Simpson, *Unio*, 319
pallida Rafinesque, *Lampsilis*, 382
paludicolor Conrad, *Unio*, 340
paludicolus Gould, *Unio*, 339
papyracea Anthony, *Anodon*, 367
paralellus Conrad, *Unio*, 339
parva (Barnes), *Carunculina*, 271, 276, 277, 371
parvus Barnes, *Unio*, 370
patrickae Bates, *Carunculina*, 370
pavonia Lea, *Anodonta*, 367
pawensis Lea, *Unio*, 340
peggyae Johnson, *Anodonta*, 272, 362, 364, 366
penicillatus (Lea), *Medionidus*, 271
pensylvanica Lamarck, *Anodonta*, 367
pepinensis Baker, *Strophitus rugosus*, 367
percoarctatus Lea, *Unio*, 315
perglobosa Baker, *Lampsilis ventricosa*, 386
perlatus Lea, *Unio*, 332
perlucens Lea, *Unio*, 317
perplicata (Conrad), *Amblema*, 270, 271
perstriatus Lea, *Unio*, 332
pertennis Lea, *Unio*, 344
planilateris Conrad, *Unio*, 308
plantii Lea, *Unio*, 340
Platynaias Walker, 343
Pleurobema Rafinesque, 299
polymorphus B. H. Wright, *Unio*, 305
porrectus Conrad, *Unio*, 339
postellii Lea, *Unio*, 316
Pressodonta Simpson, 349
prevostianus Lea, *Unio*, 373
productus Conrad, *Unio*, 333
Prolasmidonta Ortmann, 346
protensus Lea, *Unio*, 317
provancheriana Pilsbry, *Unio (Arconaia)*, 319
proximus Lea, *Unio*, 376
Pseudodontoideus Frierson, 366
Pterosyna Rafinesque, 343
pulla (Conrad), *Carunculina*, 274, 276, 277, **370**
pullatis Lea, *Unio*, 326
pullatus Lea, *Unio*, 326
pullus Conrad, *Unio*, 370
pumilus Lea, *Unio*, 301
purpurascens Lamarck, *Unio*, 305, 314
purpureus Say, *Unio*, 314
purus Lea, *Unio*, 316
pusillus Lea, *Unio*, 308
Pyganodon Crosse and Fischer, 356
pygmaeus Lea, *Unio*, 344
pyriforme (Lea), *Pleurobema*, 272, 276, 277, 302

quadrata (Lea), *Lasmigona*, 343
quadratus Lea, *Unio*, 316
quadrilaterus Lea, *Unio*, 317
quadriplicatus Sowerby, *Anodon*, 367

radiata (Gmelin), *Lampsilis (Lampsilis) radiata*, 274, 275, 277, 278, 279, **390**
radiata Gmelin, *Mya*, 390
radiata Swainson, *Unio*, 348
radiata Swainson, *Uniopsis*, 349
radiatus (Conrad), *Anodontoides*, 271, 366, 368
radiolus Lea, *Unio*, 327
raensis Lea, *Unio*, 316
raleighensis Lea, *Unio*, 317
rarisulcata Lamarck, *Unio*, 314
ratus Lea, *Unio*, 318
ravenelı Conrad, *Unio*, 325
raveneliana (Lea), *Alasmidonta*, 355
recta Lamarck, *Unio*, 380
regularis Sowerby, *Unio*, 393
rhombica Anthony, *Alasmodon*, 367
rhombula Lamarck, *Unio*, 314
rigida Wood, *Unio*, 315
rivicolus Conrad, *Unio*, 340
rivularis Conrad, *Unio*, 340
roanokensis Lea, *Unio*, 315
rosaceus Conrad, *Unio*, 389
rosaceus DeKay, *Unio*, 391
rosea Rafinesque, *Lampsilis*, 389
rostellum Lea, *Unio*, 334
rostraeformis Lea, *Unio*, 333
rostrata Valenciennes, *Unio*, 380
rostrum Lea, *Unio*, 317
roswellensis Lea, *Unio*, 316
rotulata (Wright), *Obovaria*, 273
rotundata (Lamarck), *Glebula*, 271
rubellum (Lea), *Pleurobema*, 270
rufusculus Lea, *Unio*, 308
Rugifera Simpson, 353
rugosus Swainson, *Anodon*, 367
rugulosa Wood, *Mya*, 354
rutilans Lea, *Unio*, 373

sagittiformis Lea, *Unio*, 333
salebrosus Lea, *Unio*, 316
salmonia Clessin, *Anodon*, 367
santeensis Lea, *Unio*, 318
satillaensis Lea, *Unio*, 307
satur Lea, *Unio*, 388
savannahensis Lea, *Unio*, 316
sayii Ward, *Unio*, 339
scriptum Rafinesque, *Alasmodon*, 353
sculptilis Say, *Alasmidonta*, 349
shaefferiana Lea, *Anodonta*, 367
shepardiana (Lea), *Elliptio (Elliptio)*, 274, 278, **338**
shepardianus Lea, *Unio*, 338
siliquoidea (Barnes), *Lampsilis radiata*, 279, 391
similis Lea, *Unio*, 326
simpsoni B. H. Wright, *Unio*, 327
singularis B. H. Wright, *Unio*, 327
sloatiana (Lea), *Elliptio*, 272
Solenaia Conrad, 265
sordidis Lea, *Unio*, 308
spadiceus Lea, *Unio*, 315
spinosa (Lea), *Elliptio (Canthyria)*, 274, 278, **303**
spinosus Lea, *Unio*, 303
spissus Lea, *Unio*, 307
splendida (Lea), *Lampsilis (Lampsilis)*, 274, 276, 277, 278, **393**
splendidus Lea, *Unio*, 393
squalidus Lea, *Unio*, 340
squameus Lea, *Unio*, 317
stagnalis Conrad, *Unio*, 373
striatulus Lea, *Unio*, 301
strigosus (Lea), *Elliptio*, 328, 332
strigosus Lea, *Unio*, 331
strodeanum (Wright), *Pleurobema*, 272
Strophitus Rafinesque, 366
strumosus Lea, *Unio*, 309
subangulata (Lea), *Lampsilis*, 272
subcroceus Conrad, *Unio*, 340
subcylindraceus Lea, *Unio*, 334
subellipsis Lea, *Unio*, 373
subflavus Lea, *Unio*, 316
subinflatus Conrad, *Unio complanatus*, 315
sublatus Lea, *Unio*, 326
subniger Lea, *Unio*, 316
subolivaceus Lea, *Unio*, 319
suborbiculata Say, *Anodonta*, 271, 362
subovatus Lea, *Unio*, 386
subparallelus Lea, *Unio*, 318
subplanus Conrad, *Unio*, 300, 301
subrostrata (Say), *Ligumia*, 279, 281
subsquamosus Lea, *Unio*, 318
subvexus (Conrad), *Strophitus*, 271, 274, 343, 366, 368
subviridis (Conrad), *Lasmigona (Platynaias)*, 274, 275, 276, 279, 280, 285, **343**
subviridis Conrad, *Unio*, 343
succissa (Lea), *Fusconaia*, 272
sudus Lea, *Unio*, 373
sulcidens Lamarck, *Unio*, 315
Sulcularia Rafinesque, 343, 349
swainsoni Sowerby, *Unio*, 349
symmetricus Lea, *Unio*, 339
Symphynota Simpson, 343

tappanianus Lea, *Unio*, 344
tenebrosus Conrad, *Unio*, 391
tenerus Simpson, *Unio*, 375
tennesseensis Frierson, *Strophitus undulatus*, 366
teres Conrad, *Anodonta*, 356
teres (Rafinesque), *Lampsilis*, 270
tetragona Lea, *Anodonta*, 367
tetralasmus Say, *Unio*, 276, 339
tetralasmus (Say), *Uniomerus*, 271, 274, **339**
tetricus Lea, *Unio*, 326
tortivus Lea, *Unio*, 331
tortuosus Sowerby, *Unio*, 318
Toxolasma Rafinesque, 369
triangulata (Lea), *Alasmidonta (Alasmidonta)*, 272, 274, 276, 278, **351**
triangulata Lea, *Margaritana*, 351
tryonii Lea, *Anodonta*, 357
tuomeyi Lea, *Unio*, 326, 329

uharcensis Lea, *Unio*, 318
unadilla DeKay, *Anodon*, 367
undulata (Say), *Alasmidonta (Alasmidonta)*, 274, 275, 279, 281, **349**
undulata Say, *Anodonta*, 366, 367
undulata Say, *Monodonta*, 348
undulata Say, *Unio*, 349
undulatus (Say), *Strophitus*, 274, 276, 279, 280, **367**
unicolor (Lea), *Obovaria*, 270
Unionacea Thiele, 299
Uniomerus Conrad, 339
Unionidae (Fleming) Ortmann, 299
Unioninae (Swainson) Ortmann, 299
Unionoidea Thiele, 299
Uniopsis Swainson, 348
utriculum (Lea), *Pleurobema*, 300
Utterbachia Baker, 362
Utterbackia Baker, 362
Utterbackiana Frierson, 362

vanuxemensis (Lea), *Villosa*, 277, 280, 281, 379
varicosa (Lamarck), *Alasmidonta (Decurambis)*, 274, 275, 279, **354**
varicosa Lamarck, *Unio*, 354
vaughanianus Lea, *Unio*, 375
vaughanianus Sowerby, *Unio*, 380
ventricosus Barnes, *Unio*, 386
verutus Lea, *Unio*, 327
vestitus Lea, *Unio*, 308
vibex (Conrad), *Villosa*, 271, 274, 276, **373**
vibex Conrad, *Unio*, 373
vicinus Lea, *Unio*, 315
Villosa Frierson, 371, 372
villosa (Wright), *Villosa*, 272, **372**
villosus Simpson, *Lampsilis*, 372
villosus B. H. Wright, *Unio*, 372
violaceus Spengler, *Unio*, 314
virens Lea, *Unio*, 316
virgata Conrad, *Anodonta*, 367
virginea Frierson, *Unio*, 391
virginiana Lamarck, *Unio*, 315
virginiana Simpson, *Unio*, 391
virgulata Lea, *Anodonta*, 356
viridans Lea, *Unio*, 327
viridicatus Lea, *Unio*, 326
viridiradiatus Lea, *Unio*, 326
viridis Rafinesque, *Lasmigona*, 343
viridis Conrad, *Unio*, 344
viridulus Lea, *Unio*, 333

waccamawensis (Lea), *Elliptio (Elliptio)*, 274, 278, **313**
waccamawensis Lea, *Unio*, 313
walkeri (Wright), *Medionidus*, 272
wardiana Lea, *Anodonta*, 367
watereensis Lea, *Unio*, 325
websterii B. H. Wright, *Unio*, 310
weldonensis Lea, *Unio*, 317
wheatleyi Lea, *Unio*, 315
whiteianus Lea, *Unio*, 326
williamsii Lea, *Anodonta*, 357
winnebagoensis Baker, *Lampsilis ventricosa*, 386
winnebagoensis Baker, *Strophitus rugosus*, 367
wrightiana (Walker), *Alasmidonta*, 273, 350
wrightianus Clench and Turner, *Strophitus*, 351
wrightianus Walker, *Strophitus*, 348

yadkinensis Lea, *Unio*, 318

PLATE 1

The Southeastern United States

A.M. The solid line indicates the limit of the Appalachian Mountains. The divide is somewhat to the west of it.

P.P. Piedmont Plateau. The line thus indicated, – – – – –, is the Fall Line.

C.P. Coastal Plain. The line thus indicated, · – · – ·, is the limit of the Brandywine (maximum) interglacial (now thought to be Upper Miocene) flooding, and is, in part, conjectural.

A. Area of stream capture of the New River and the North Fork of the Roanoke River.

B. Area of confluence of the headwaters of the Alabama-Coosa, Apalachicola and Savannah River systems.

C. Area of suspected stream confluence between Uphauppee Creek of the Alabama-Coosa River system and Uchee Creek of the Apalachicola River system.

D. Area of suspected confluence of the headwaters of the Choctawhatchee River and the Chattahoochee River.

The Principal Drainage Systems

1. ALABAMA-COOSA RIVER SYSTEM
    2. Coosa River Drainage
    3. Tallapoosa River Drainage

Apalachicolan Region

4. ESCAMBIA RIVER SYSTEM
5. YELLOW RIVER SYSTEM
6. CHOCTAWHATCHEE RIVER SYSTEM
7. APALACHICOLA RIVER SYSTEM
    8. Chattahoochee River Drainage
    9. Flint River Drainage
10. OCHLOCKONEE RIVER SYSTEM
11. ECONFINA RIVER SYSTEM
12. SUWANNEE RIVER SYSTEM
13. ST. MARYS RIVER SYSTEM
14. SATILLA RIVER SYSTEM

Southern Atlantic Slope Region

15. ALTAMAHA RIVER SYSTEM
    16. Ocmulgee River Drainage
    17. Oconee River Drainage
18. OGEECHEE RIVER SYSTEM
19. SAVANNAH RIVER SYSTEM
20. EDISTO RIVER SYSTEM
21. COOPER-SANTEE RIVER SYSTEM
    22. Saluda River Drainage
    23. Broad River Drainage
    24. Catawba River Drainage
25. BLACK RIVER SYSTEM
26. PEDEE RIVER SYSTEM
    27. Yadkin River Drainage
28. WACCAMAW RIVER SYSTEM
29. CAPE FEAR RIVER SYSTEM
30. NEUSE RIVER SYSTEM
31. PAMLICO RIVER SYSTEM
32. ROANOKE RIVER SYSTEM
    33. Dan River Drainage
    34. Roanoke River Drainage
35. CHOWAN RIVER SYSTEM
36. JAMES RIVER SYSTEM

Northern Atlantic Slope Region

37. YORK RIVER SYSTEM
38. RAPPAHANNOCK RIVER SYSTEM
39. POTOMAC RIVER SYSTEM
    40. Shenandoah River Drainage

SOUTHEASTERN UNITED STATES
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PLATE 2

Pleurobema (Lexingtonia) collina (Conrad)

Fig. 1. *Unio collinus* Conrad. North [= Maury] River, a branch of the James River [Rockbridge County], Virginia. Lectotype ANSP 41007. Length 46 mm, height 30 mm, width 19 mm (nat. size).

Fig. 2. [James River] USNM 84376. Length 18.8 mm. Specimen sprayed with ammonium chloride vapor. After Boss and Clench (1967, pl. 15, fig. 2).

Pleurobema (Lexingtonia) masoni (Conrad)

Fig. 3. *Unio masoni* Conrad. Savannah River, Augusta [Richmond County], Georgia. Holotype ANSP 41333. Length 26.6 mm, height 19.3 mm, width 13.3 mm (nat. size).

Fig. 4. Mill Race, 2 mi. N of Sardis, Burke County, Georgia, MCZ 234387. Length 47 mm, height 28 mm, width 19 mm (nat. size).

Fig. 5. *Unio masoni* Conrad. Savannah River, Augusta [Richmond County], Georgia. Paratype ANSP 41332. Length 37 mm, height 26 mm, width 16 mm (nat. size).

Fig. 6. *Unio castus* Lea. South Carolina. Holotype USNM 84782. Length 40 mm, height 27 mm, width 17 mm (nat. size).

Fig. 7. *Unio brimleyi* Wright. [Walnut Creek of] Neuse River, Raleigh [Wake County], North Carolina. Lectotype USNM 149651. Length 38 mm, height 29 mm, width 15 mm (nat. size).

Fig. 8. *Unio merus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85698. Length 38 mm, height 29 mm, width 15 mm (nat. size).

Fig. 9. *Unio pumilus* Lea. Black River [about 10 mi. W of Benson, Johnston County], North Carolina. Holotype USNM 84545. Length 28 mm, height 20 mm, width 13 mm (nat. size).

Fig. 10. *Unio striatulus* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 84548. Length 39 mm, height 28 mm, width 17 mm (nat. size).

Elliptio (Canthyria) spinosa (Lea)

Fig. 11. Altamaha River, 4 mi. NE of Jesup, Wayne County, Georgia. MCZ 234055. Length 59 mm, height 37 mm, width 22 mm (approximately 1.2 ×).

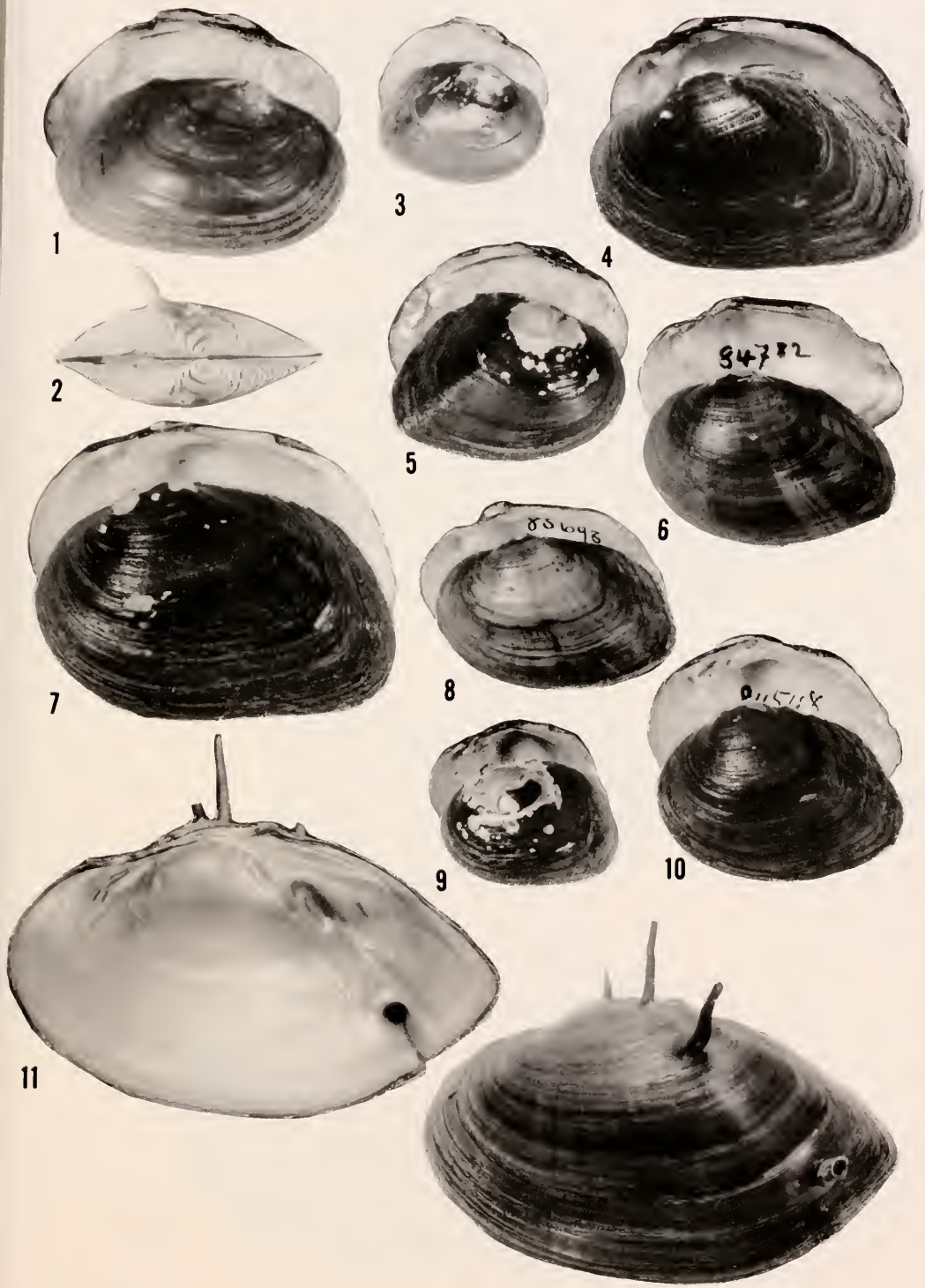
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PLATE 3

Elliptio (Elliptio) crassidens crassidens (Lamarck)

Fig. 1. *Unio lehmanii* Wright. St. Marys River [Nassau County], Florida. Lectotype USNM 149650. Length 60 mm, height 40 mm, width 24 mm (nat. size).

Fig. 2. *Unio polymarphus* Wright. Spanish Creek [a tributary of the St. Marys River W of Folkston], Charletan County, Georgia. Lectotype USNM 152060. Length 75 mm, height 46 mm, width 29 mm (slightly reduced).

Fig. 3. Spanish Creek, Charletan County, Georgia. MCZ 269228. Length 62 mm, height 40 mm, width 30 mm (slightly reduced).

Fig. 4. As above. Length 94 mm, height 57 mm, width 38 mm (slightly reduced).

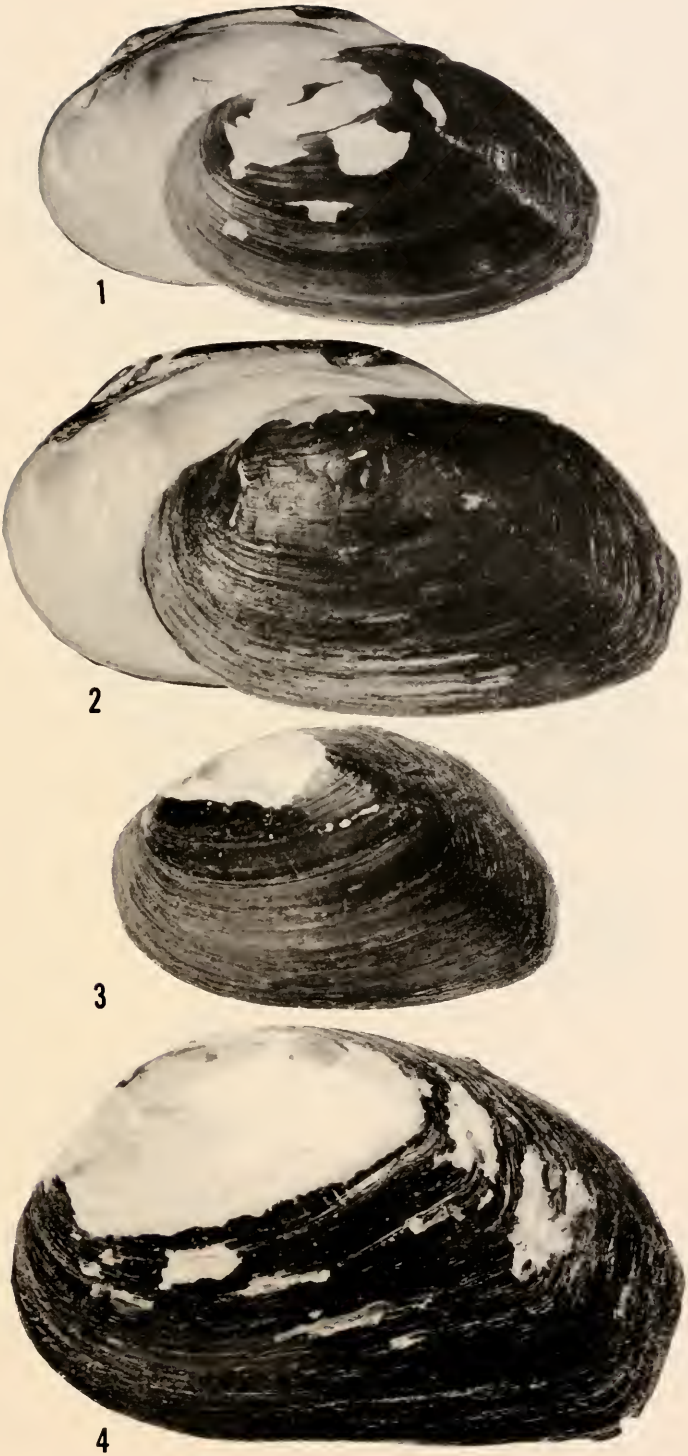
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PLATE 4

Elliptio (*Elliptio*) *crassidens downiei* (Lea)

Fig. 1. *Unio downiei* Lea. Buck Lake, a bayou of the Satilla River, Wayne [Brantly] County, Georgia. Holotype USNM 84854. Length 84 mm, height 49 mm, width 36 mm (slightly reduced).

Fig. 2. *Unio satillaensis* Lea. Satilla River, Camden County, Georgia. Holotype USNM 84855. Length 75 mm, height 45 mm, width 30 mm (slightly reduced).

Fig. 3. Satilla River, 3 mi. S of Hortense, Brantly County, Georgia. MCZ 237460. Length 27 mm, height 16 mm, width 8 mm (nat. size).

Fig. 4. *Unio spissus* Lea. Satilla River, Wayne County, Georgia. Holotype USNM 84853. Length 76 mm, height 57 mm, width 40 mm (approximately nat. size).

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PLATE 5

Elliptio (Elliptio) congaraea (Lea)

Fig. 1. *Unio congaraeus* Lea. Congaree River [Cooper-Santee River system], South Carolina. Holotype USNM 85693. Length 41 mm, height 25 mm, width 14 mm (slightly reduced).

Fig. 2. *Unio fulvus* Lea. South Carolina. Holotype USNM 85679. Length 40 mm, height 21 mm, width 15 mm (slightly reduced).

Fig. 3. *Unio vestitus* Lea. Ogeechee River [Georgia]. Holotype USNM 85332. Length 39 mm, height 25 mm, width 15 mm (nat. size).

Fig. 4. *Unio forbesianus* Lea. Savannah River, Georgia. Holotype USNM 84542. Length 45 mm, height 31 mm, width 29 mm (nat. size).

Fig. 5. *Unio lecontianus* Lea. Canoochee River, Liberty County, Georgia. Holotype USNM 84852. Length 70 mm, height 45 mm, width 29 mm (slightly reduced).

Fig. 6. *Unio dorsatus* Lea. Catawba River, North Carolina. Holotype USNM 84494. Length 57 mm, height 40 mm, width 23 mm (nat. size).

Fig. 7. *Unio moussanianus* Lea. Georgia. Holotype USNM 85168. Length 72 mm, height 49 mm, width 28 mm (slightly reduced).

Fig. 8. *Unio carvus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 84539. Length 62 mm, height 40 mm, width 25 mm (nat. size).

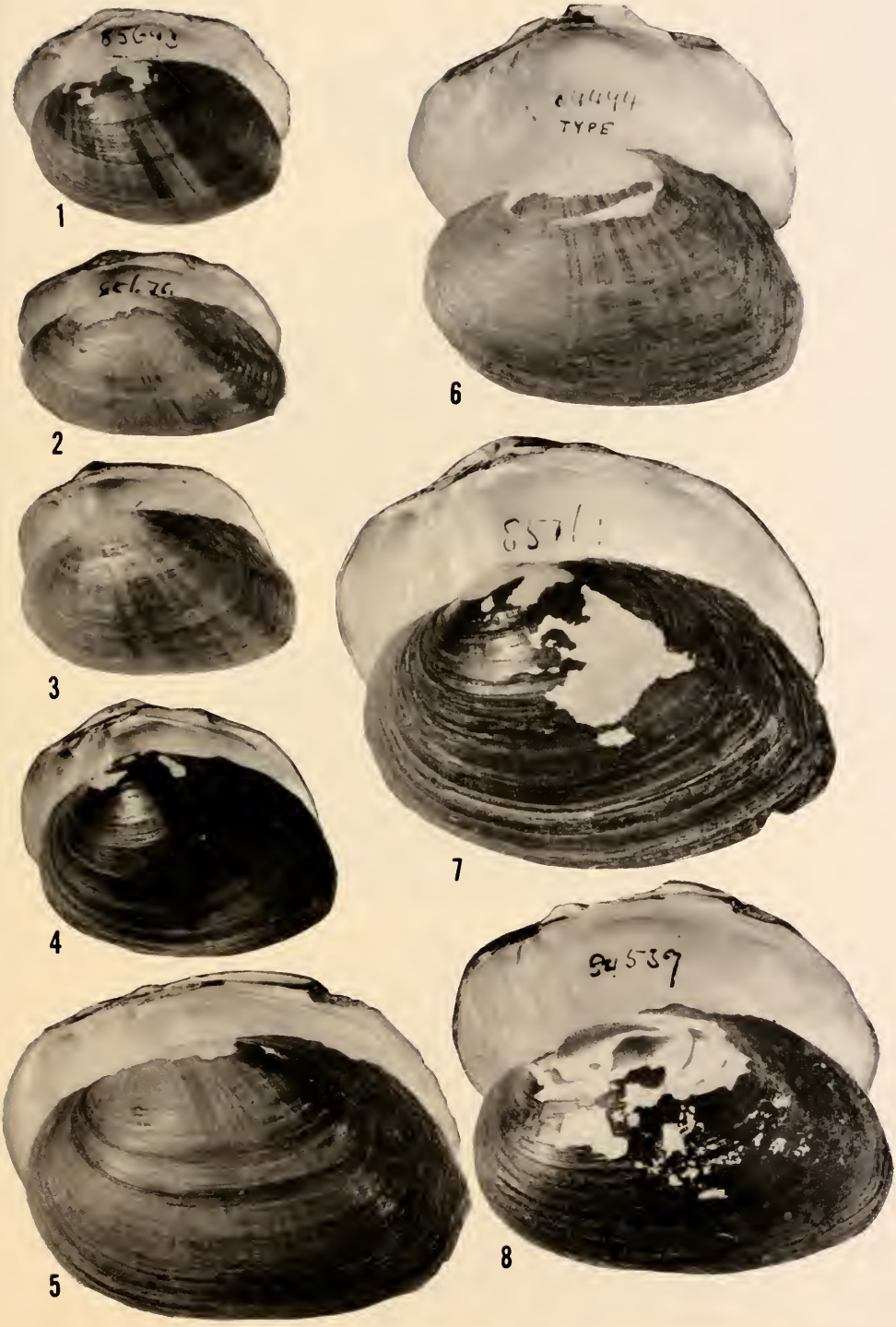

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PLATE 6

Elliptio (*Elliptio*) *dariensis* (Lea)

Fig. 1. House Creek, Bowens Mills, 9 mi. N of Fitzgerald, Ben Hill County, Georgia. MCZ 234237. Length 41 mm, height 23 mm, width 14 mm (not. size).

Fig. 2. *Unio dariensis* Lea. [Altamaha River] near Darien [McIntosh County], Georgia. Holotype USNM 85691. Length 78 mm, height 55 mm, width 28 mm (slightly reduced).

Fig. 3. House Creek, Bowens Mill, 9 mi. N of Fitzgerald, Ben Hill County, Georgia. MCZ 234237. Length 76 mm, height 45 mm, width 26 mm (not. size).

Fig. 4. As above. Length 98 mm, height 58 mm, width 35 mm (not. size).

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PLATE 7

Elliptio (*Elliptia*) *fraterna* (Lea)

Fig. 1. *Unio fraternus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85396. Length 60 mm, height 31 mm, width 16 mm (slightly reduced).

Fig. 2. *Unio fraternus* Lea. [Chattahoochee River] Columbus [Muscogee County], Georgia. Paratype USNM 85398. Length 69 mm, height 34 mm, width 17 mm (slightly reduced).

Fig. 3. *Unio anthonyi* Lea. Florida. Holotype USNM 84986. Length 58 mm, height 35 mm, width 22 mm (slightly reduced).

Fig. 4. Flat Creek, 8 mi. SW of Samson, Geneva County, Alabama. MCZ 186967. Length 75 mm, height 38 mm, width 20 mm.

Fig. 5. *Elliptio mcmichaeli* Clench and Turner. Choctawhatchee River, 8 mi. W of Miller Cross Roads, Holmes County, Florida. Holotype MCZ 191922. Length 91 mm, height 50 mm, width 27 mm.

Elliptio waccamawensis (Lea)

Fig. 6. *Unio waccamawensis* Lea. Lake Waccamaw, North Carolina. Holotype USNM 84437. Length 36 mm, height 17 mm, width 16 mm (nat. size).

Fig. 7. Canal beside Lake Waccamaw, 1 mi. NNW of Dupree Londing, Columbus County, North Carolina. MCZ 214235. Length 89 mm, height 45 mm, width 28 mm (approximately not. size).

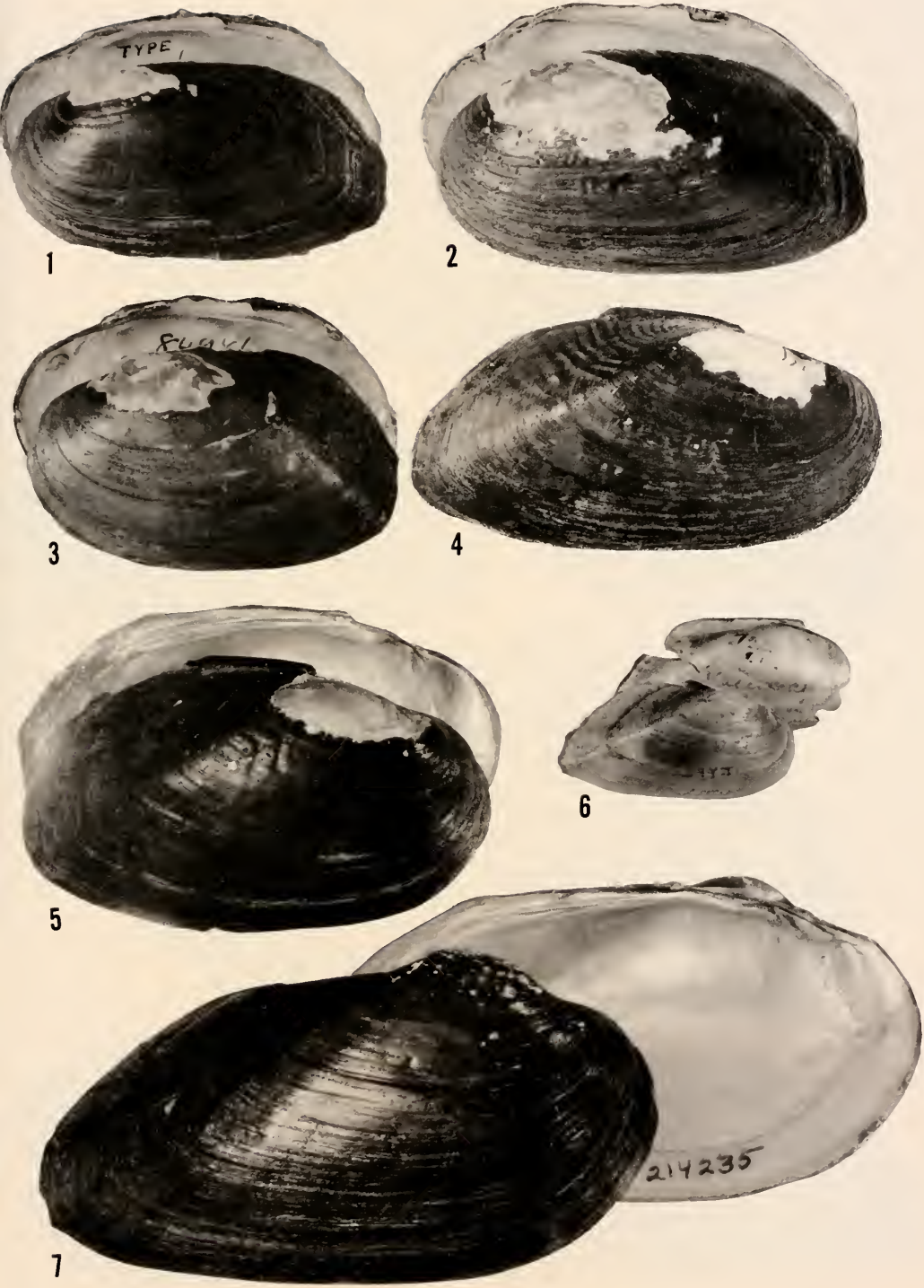
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PLATE 8

Elliptio (*Elliptio*) *complanata* (Lightfoot)

Fig. 1. Savannah River, 7 mi. NE of Newington, Screven County, Georgia. MCZ 269257. Length 99 mm, height 50 mm, width 28 mm (slightly enlarged).

Fig. 2. Turkey Creek, 4 mi. NE of Allentown [Altamaha River system], Wilkinson County, Georgia. MCZ 234355. Length 73 mm, height 36 mm, width 18 mm (nat. size).

Fig. 3. *Unio quadrilaterus* Lea. Neuse River, near [6 mi. E of] Raleigh, [Wake County], North Carolina. Holotype USNM 85385. Length 60 mm, height 36 mm, width 20 mm (slightly reduced).

Fig. 4. *Unio roanokensis* Lea. Roanoke River [road between Norfolk, Virginia, and Tarboraugh, North Carolina]. Holotype USNM 85423. Length 119 mm, height 57 mm, width 29 mm (slightly reduced).

Fig. 5. *Unio mediocris* Lea. Neuse River, [6 mi. E of] Raleigh [Wake County], North Carolina. Holotype USNM 85611. Length 57 mm, height 30 mm, width 19 mm (slightly reduced).

Fig. 6. North shore, Lake Waccamaw, town of Lake Waccamaw, Columbus County, North Carolina. MCZ 258813. Length 60 mm, height 31 mm, width 18 mm (approximately nat. size).

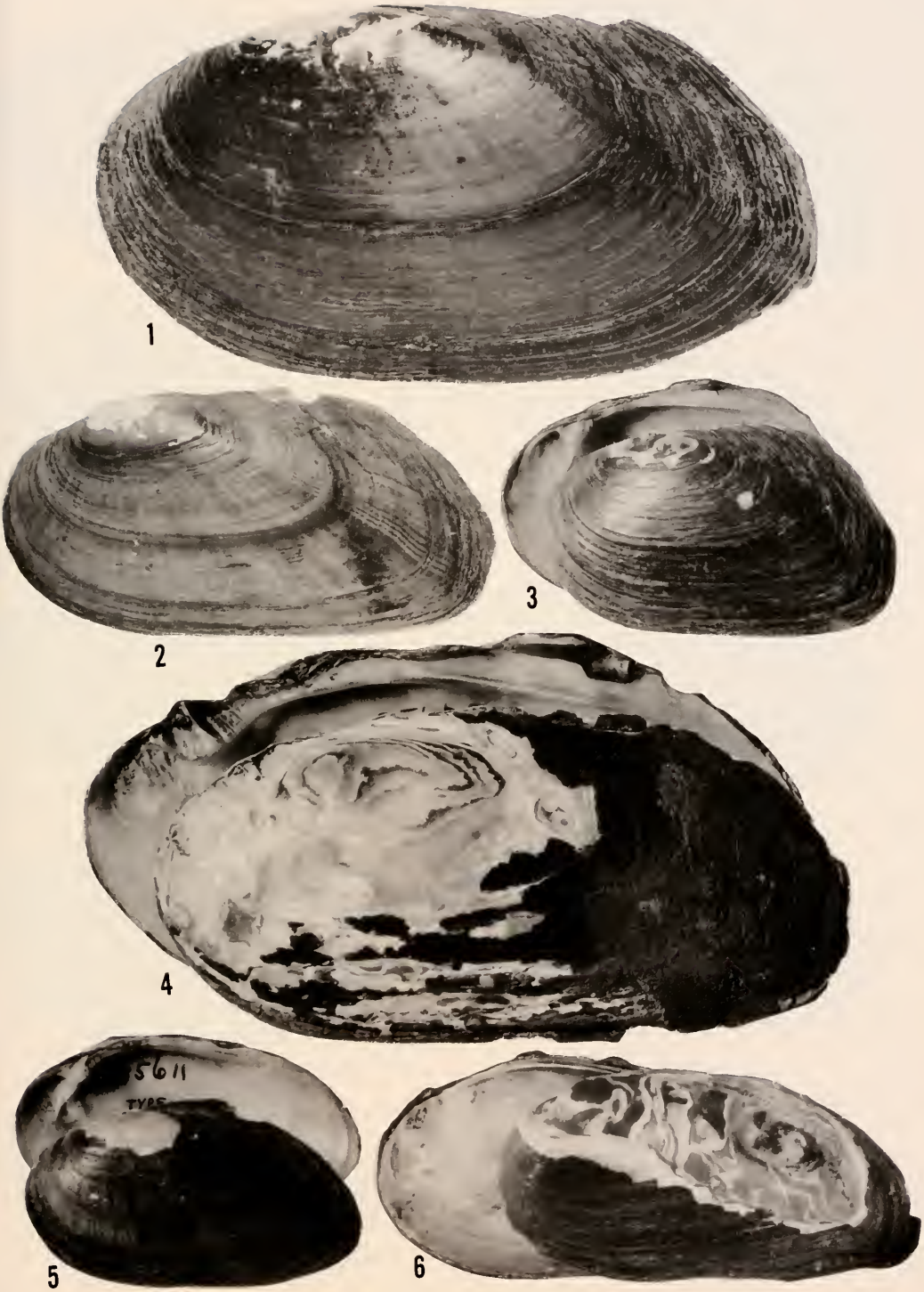
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PLATE 9

Elliptio (Elliptio) hapetanensis (Lea)

Fig. 1. *Unio inusitatis* Lea. Swift Creek, below Macon [Bibb County], Georgia. Holotype USNM 85531. Length 57 mm, height 32 mm, width 19 mm (slightly reduced).

Fig. 2. *Unio hapetanensis* Lea. [Altamaha River], Hapetan, near Darien [McIntash County], Georgia. Holotype USNM 85391. Length 84 mm, height 43 mm, width 20 mm (slightly reduced).

Elliptio (Elliptio) icterina (Conrad)

Fig. 3. *Unio icterinus* Conrad. Savannah River, opposite Augusta [Richmond County], Georgia. Holotype ANSP 41381. Length 55 mm, height 28 mm, width 18 mm (approximately nat. size).

Fig. 4. *Unio lugubris* Lea. [Altamaha River], Hapetan, near Darien [McIntash County], Georgia. Holotype USNM 85638. Length 53 mm, height 37 mm, width 22 mm (slightly enlarged).

Fig. 5. *Unio tuomeyi* Lea. Abbeville District [Savannah River drainage]. South Carolina. Holotype USNM 85669. Length 65 mm, height 33 mm, width 19 mm (slightly reduced).

Fig. 6. *Unio opacus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85546. Length 66 mm, height 37 mm, width 24 mm (slightly reduced).

Fig. 7. *Unio hastatus* Lea. New Market, Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 86013. Length 66 mm, height 28 mm, width 17 mm (slightly reduced).

Fig. 8. *Unio abnubilus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85646. Length 65 mm, height 38 mm, width 23 mm (slightly reduced).

Fig. 9. *Unio similis* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85653. Length 57 mm, height 31 mm, width 20 mm (slightly reduced).

Fig. 10. *Unio aequatus* Lea. Buckhead Creek, Burke County, Georgia. Holotype USNM 85561. Length 66 mm, height 38 mm, width 21 mm (slightly reduced).

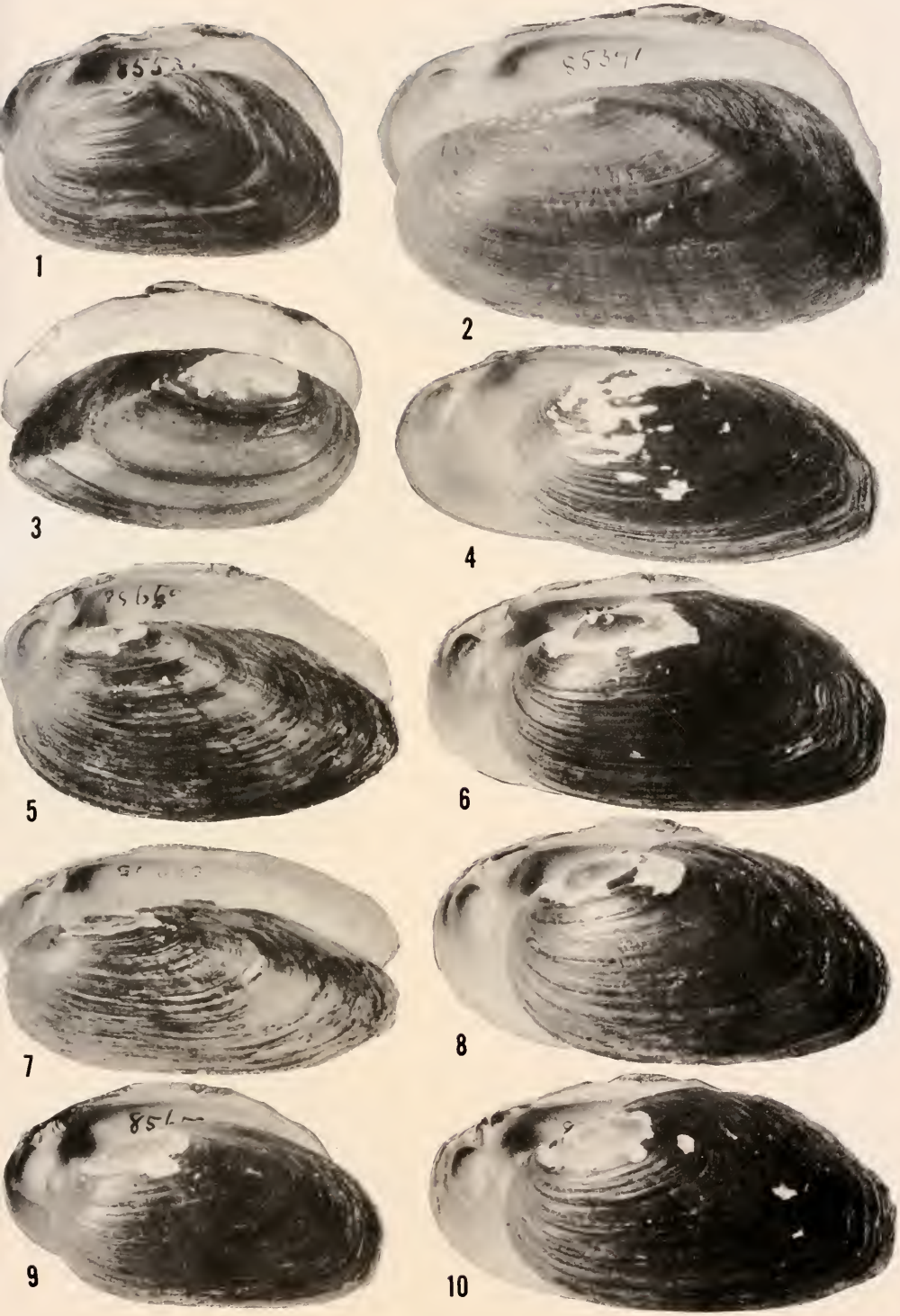
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PLATE 10

Elliptio (*Elliptio*) *icterina* (Conrad)

Fig. 1. *Unio micans* Lea. Catawba River, Gaston County, Narth Carolina. Holotype USNM 85077. Length 44 mm, height 23 mm, width 14 mm (slightly reduced).

Fig. 2. *Unio ocmulgéensis* Lea. Little Ocmulgee River, Lumber City, [Telfair County], Georgia. Holotype USNM 85901. Length 104 mm, height 50 mm, width 35 mm (slightly reduced).

Fig. 3. *Unio confertus* Lea. Santee Canal, South Carolina, from J. Lewis. Metotype USNM 85634. Length 60 mm, height 33 mm, width 22 mm (slightly reduced).

The holotype was not located. This specimen, identified by Lea, is almost the same width and height as the original specimen, though the latter was more inflated, measuring 28 mm in width.

Elliptio (*Elliptio*) *arctata* (Conrad)

Fig. 4. *Unio arctatus* Conrad. Alabama River, Alabama. Lectotype ANSP 41356. Length 55 mm, height 22 mm, width 14 mm (nat. size).

Fig. 5. *Unio strigosus* Lea. Chattahoachee River, Columbus [Muscogee County], Georgia. Holotype USNM 85890. Length 56 mm, width 24 mm, height 13 mm (slightly reduced).

Fig. 6. *Unio lazarus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 86155. Length 52 mm, height 23 mm, width 12 mm (slightly reduced).

Fig. 7. *Unio perstriatus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85892. Length 57 mm, height 25 mm, width 12 mm (slightly reduced).

Fig. 8. *Unio gracilentus* Lea. Catawba River, Gaston County, North Caralina. Holotype USNM 85976. Length 71 mm, height 30 mm, width 13 mm (slightly reduced).

Fig. 9. *Unio perlatus* Lea. Cape Fear River, Black Rock Landing [= 2 mi. S of Kings Bluff, Bladen County], North Carolina. Holotype USNM 86006. Length 66 mm, height 22 mm, width 12 mm (slightly reduced).

Elliptio (*Elliptio*) *lanceolata* (Lea)

Fig. 10. *Unio productus* Conrad. Savannah River, Augusta [Richmond County, Georgia]. Holotype ANSP 41397. Length 66 mm, height 26 mm, width 16.5 mm (approximately nat. size).

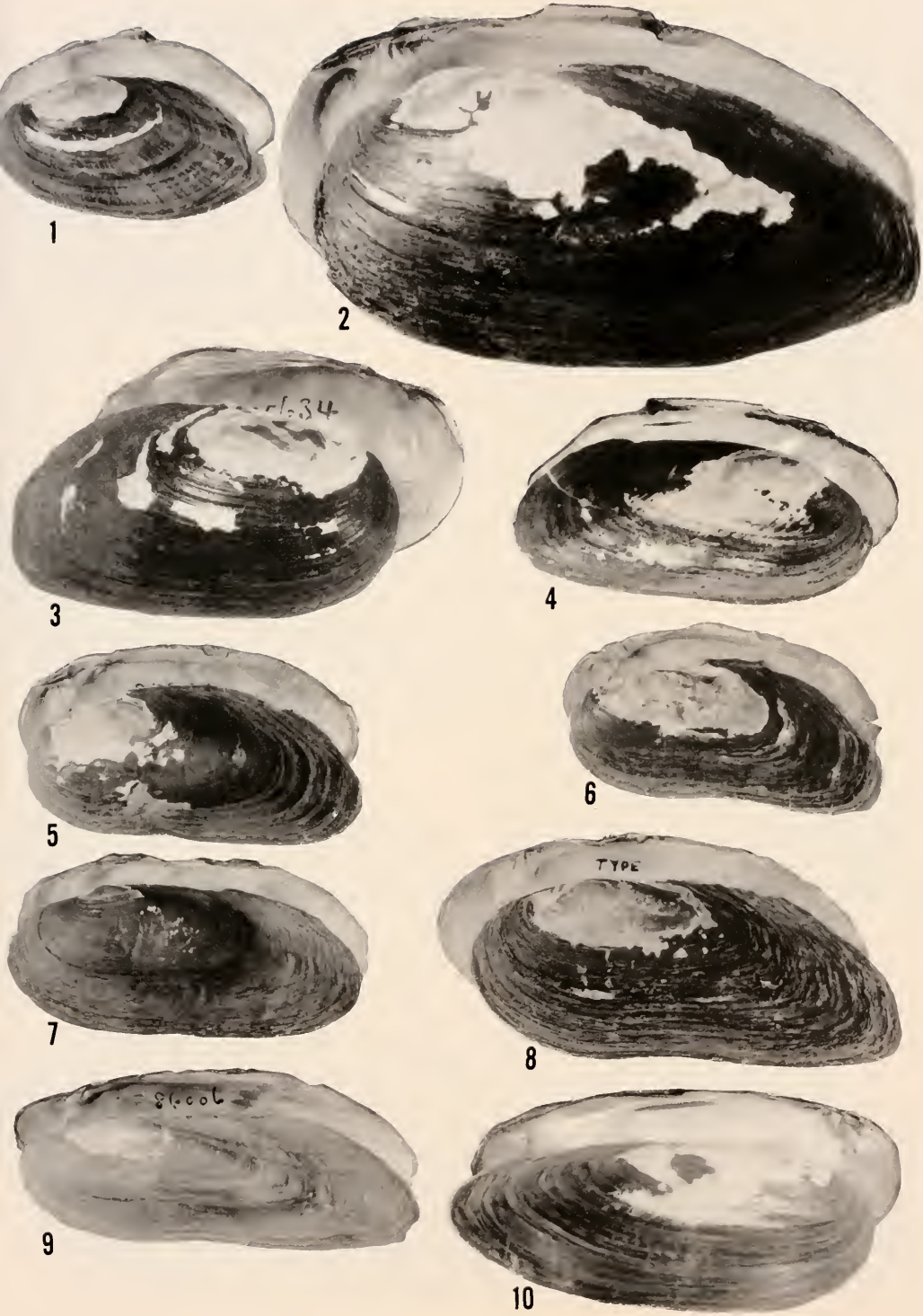
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PLATE 11

Elliptio (*Elliptio*) *lanceolata* (Lea)

Fig. 1. *Unio subcylindraceus* Lea. Racky Creek, near Macan [Bibb County], Georgia. Halatype USNM 85863. Length 95 mm, height 41 mm, width 36 mm (slightly reduced).

Fig. 2. *Unio lanceolatus* Lea. Tar River, Tarboraugh [Edgecombe County], Narth Carolina. Halotype USNM 85905. Length 41 mm, height 18 mm, width 11 mm (slightly reduced).

Fig. 3. *Unio angustatus* Lea. Cooper River, South Carolina. Holatype USNM 85896. Length 72 mm, height 29 mm, width 17 mm (slightly reduced).

Fig. 4. *Unio emmonsii* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 86028. Length 110 mm, height 46 mm, width 26 mm (slightly reduced).

Fig. 5. *Unio hazelhurstianus* Lea. Satilla River, Camden County, Georgia. Halotype USNM 86009. Length 78 mm, height 35 mm, width 22 mm (slightly reduced).

Fig. 6. *Unio fisherianus* Lea. Head of Chester River [Kent County], Maryland. Holotype USNM 86002. Length 70 mm, height 29 mm, width 15 mm (slightly reduced).

Elliptia (*Elliptio*) *shepardiana* (Lea)

Fig. 7. Ocmulgee River, 1 mi. S of Lumber City, Telfair Caunty, Georgia. MCZ 234042. Length 127 mm, height 29 mm, width 15 mm (slightly enlarged).

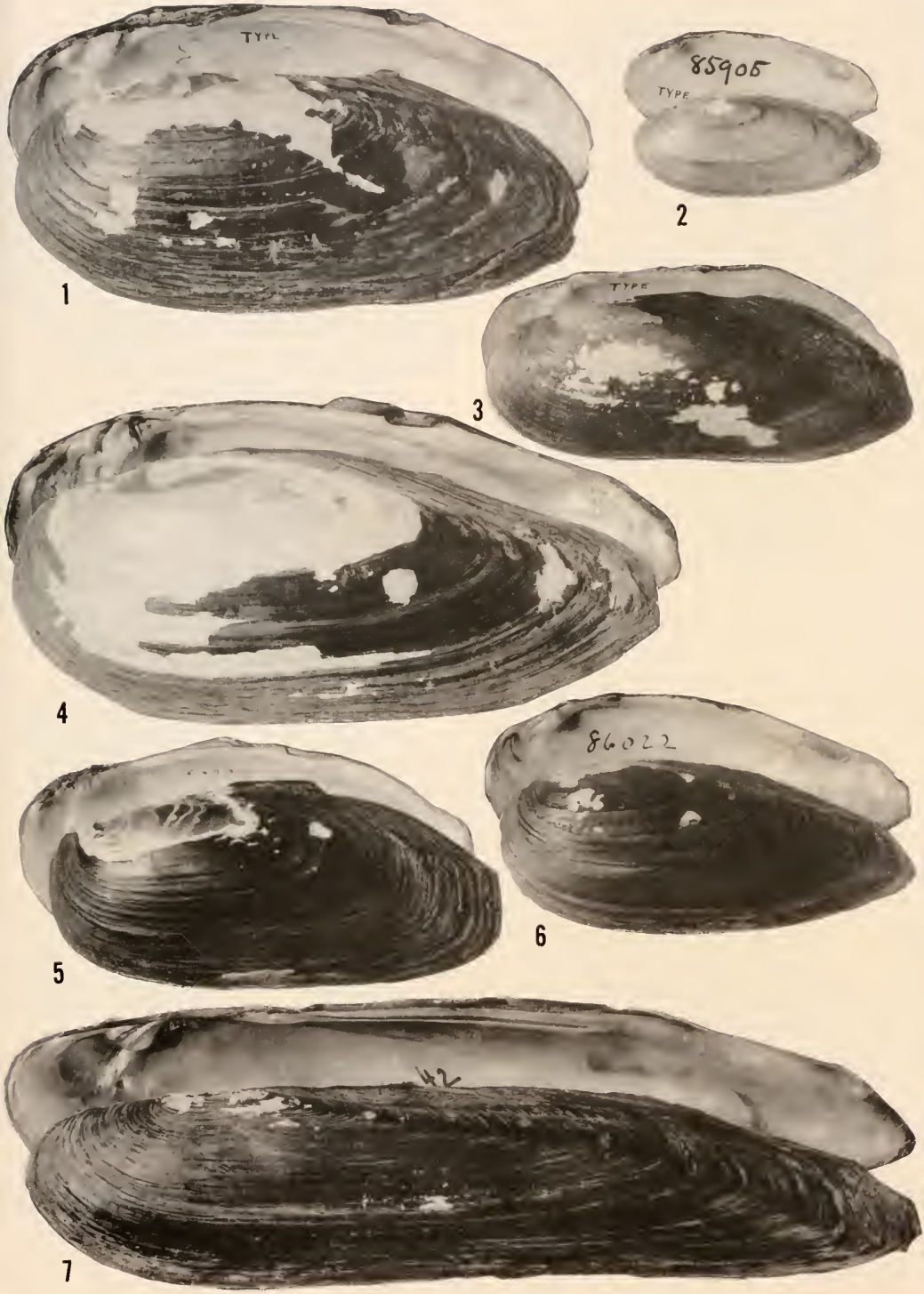
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PLATE 12

Uniamerus tetralasmus (Say)

Fig. 1. *Unio abesus* Lea. Little Ogeechee River [Hancock County], Georgia. Holotype USNM 85366. Length 82 mm, height 50 mm, width 35 mm (slightly reduced).

Fig. 2. *Unio bisselianus* Lea. Bissels Pond, Charlotte [Mecklenburg County], North Carolina. Holotype USNM 85373. Length 69 mm, height 40 mm, width 24 mm (slightly reduced).

Fig. 3. *Unio squalidus* Lea. Roanoke River, near Weldon [Halifax County], North Carolina. Holotype USNM 85376. Length 52 mm, height 30 mm, width 18 mm (slightly reduced).

Fig. 4. *Unio cicur* Lea. Little Ocmulgee River, Georgia. Holotype USNM 85532. Length 41 mm, height 25 mm, width 17 mm (slightly reduced).

Fig. 5. *Unio ineptus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85326. Length 33 mm, height 18 mm, width 10 mm (slightly reduced).

Fig. 6. *Unio pawensis* Lea. Beaver Creek [into ?], Catawba Run [Gaston and Mecklenburg Counties], North Carolina. Holotype USNM 85380. Length 74 mm, height 42 mm, width 29 mm (slightly reduced).

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Fig. 7. *Unio pertenuis* Lea. Neuse River, near [6 mi. E of] Raleigh [Wake County], North Carolina. Holotype USNM 86139. Length 35 mm, height 22 mm, width 13 mm (slightly reduced).

Fig. 8. *Unio hyalinus* Lea. [James River drainage], Richmond [Henrico County], Virginia. Holotype USNM 86131. Length 35 mm, height 21 mm, width 12 mm (slightly reduced).

Fig. 9. *Unio charlottensis* Lea. [Sugar Creek], near Charlotte, Mecklenburg County, North Carolina. Holotype USNM 85402. Length 101 mm, height 58 mm, width 34 mm (slightly reduced).

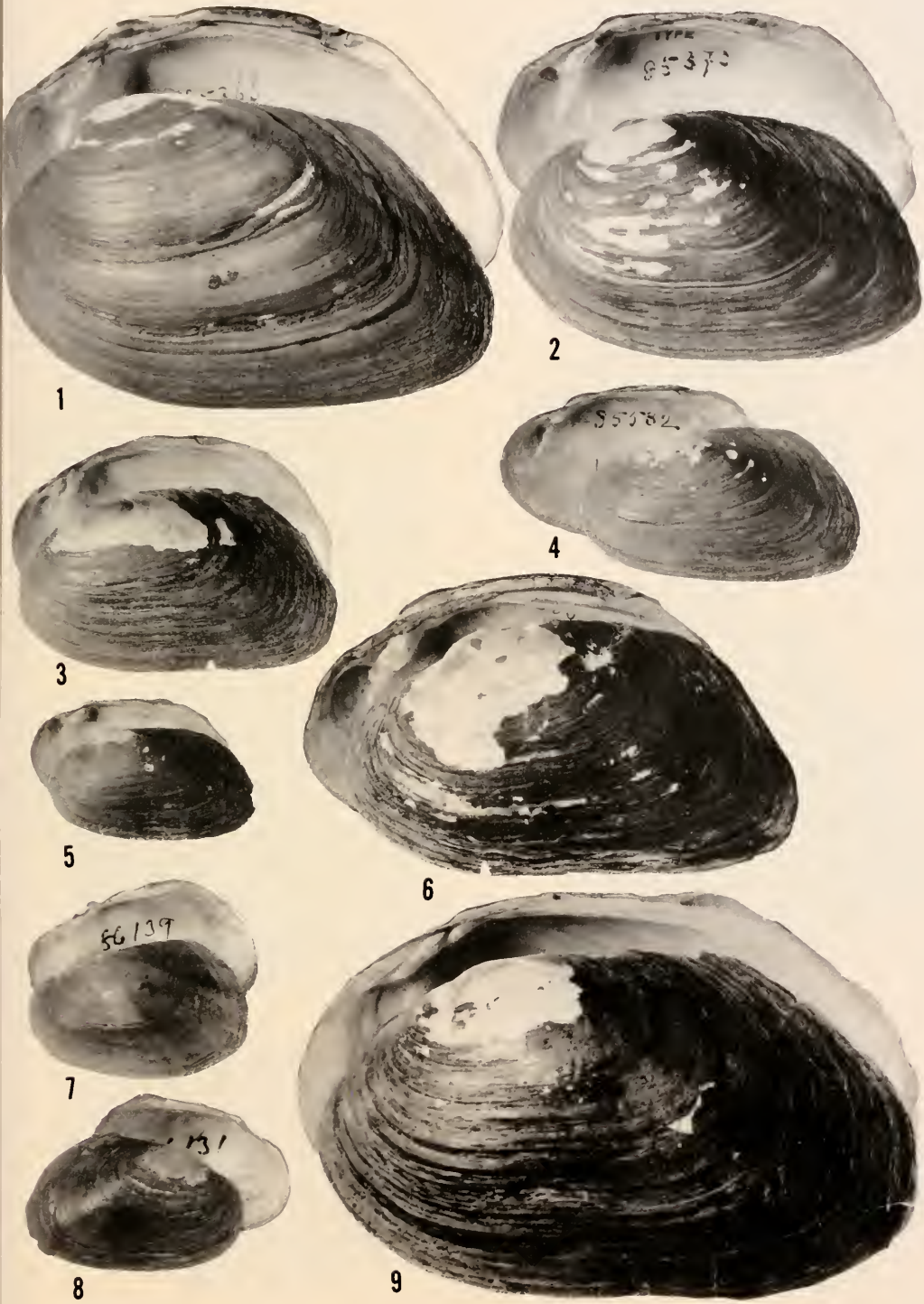
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PLATE 13

Lasmigona (*Platynaias*) *subviridis* (Conrad)

Fig. 1. *Unio decoratus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 83972. Length 60 mm, height 37 mm, width 19 mm (slightly reduced).

Alasmidonta (*Prolasmidonta*) *heterodan* (Lea)

Fig. 2. Neuse River [6 mi. E of] Raleigh [Wake County], North Carolina. MCZ 231191. Length 34 mm, height 19 mm, width 14 mm (1.5 ×).

Alasmidonta (*Alasmidonta*) *undulata* (Say)

Fig. 3. Nottoway River, 3 mi. E of Rawlings, Brunswick County, Virginia. MCZ 237455. Length 54 mm, height 32 mm, width 23 mm (approximately nat. size).

Fig. 4. James River, opposite Maidens, Goochland County, Virginia. MCZ 261313. Length 29 mm, height 19 mm, width 13 mm (1.5 ×).

Alasmidonta (*Alasmidonta*) *triangulata* (Lea)

Fig. 5. *Margaritana triangulata* Lea. Upper Chattahoochee [River], Georgia. Holotype USNM 86249. Length 57 mm, height 38 mm, width 31 mm (nat. size).

Fig. 6. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 237453. Length 48 mm, height 32 mm, width 27 mm (slightly enlarged).

Alasmidonta (*Alasmidonta*) *arcula* (Lea)

Fig. 7. *Margaritana arcula* Lea. Altamaha [River], Liberty [now Long] County, Georgia. Holotype USNM 86170. Length 57 mm, height 44 mm, width 41 mm (nat. size).

Fig. 8. Altamaha River, 4 mi. NE of Jesup, Wayne County, Georgia. MCZ 237551. Length 50 mm, height 43 mm, width 38 mm (slightly enlarged).

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PLATE 14

Alasmidonta (*Decurambis*) *varicosa* (Lamarck)

Fig. 1. Turkey Creek, 8 mi. NW of Edgefield, Edgefield County, South Carolina. MZUM 58024. Length 44 mm, height 26 mm, width 18 mm (slightly reduced).

Fig. 2. North Fork of Shenandoah River, E of Woodstock, Shenandoah County, Virginia. MCZ 216721. Length 45 mm, height 25 mm, width 18 mm (2×).

Anodonta (*Pyganodon*) *cataracta cataracta* Say

Fig. 3. *Anodonta daliaris* Lea. Stewarts Mill Dam, Union County, North Carolina. Topotype MZUM 103859, from the original lot collected by C. M. Wheatley. Lea saw only the holotype in the ANSP 126522a. Length 111 mm, height 67 mm, width 50 mm (slightly reduced).

Fig. 4. *Anodonta dariensis* Lea. Swift Creek, near Macon [Bibb County], Georgia. Holotype USNM 86600. Length 107 mm, height 58 mm, width 49 mm (slightly reduced).

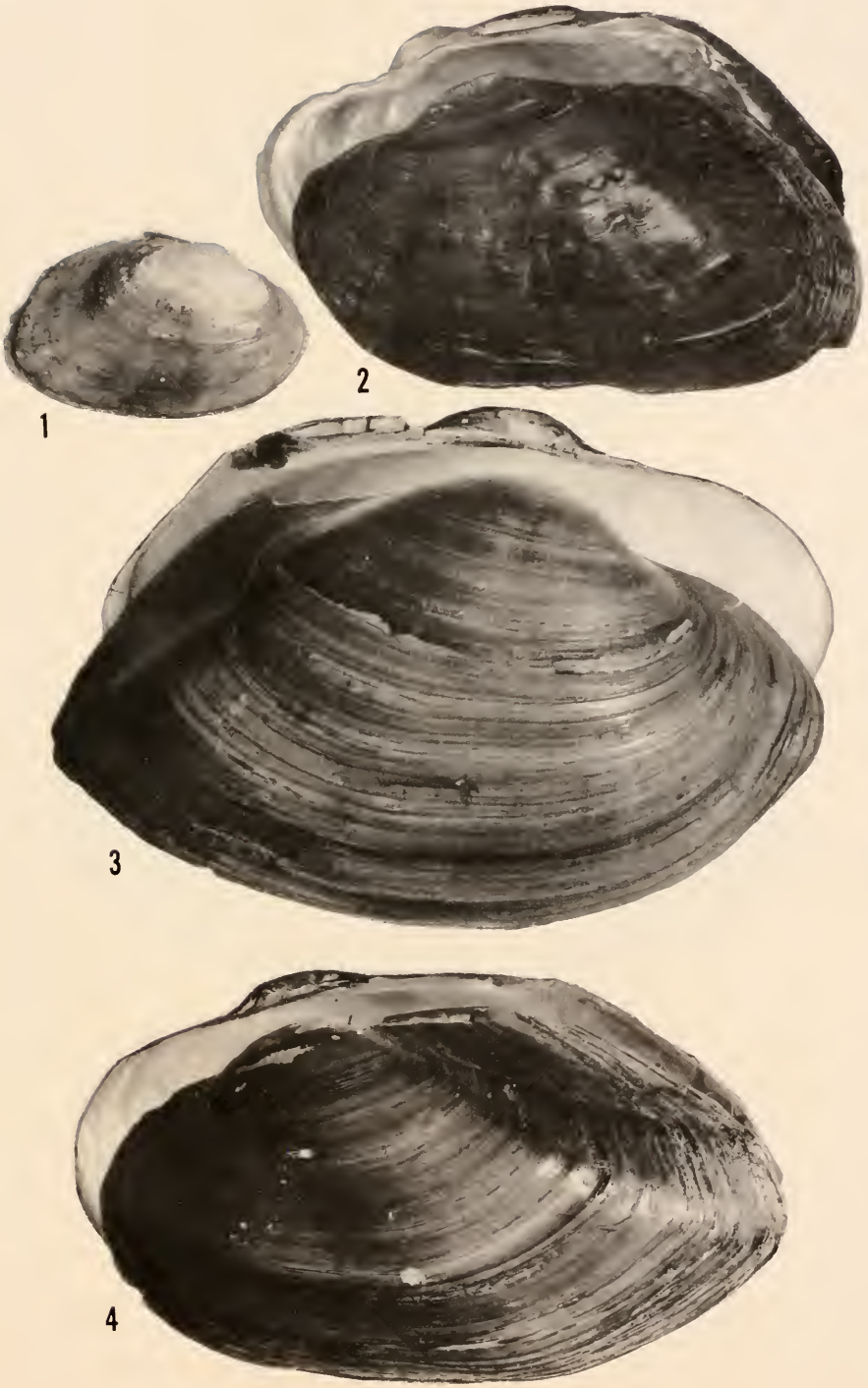
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PLATE 15

Anodonta (Pyganodon) cataracta cataracta Say

Fig. 1. *Anodonta virgulata* Lea. Roanoke River, Weldon [Halifax County], North Carolina. Holotype USNM 86593. Length 78 mm, height 44 mm, width 33 mm.

Anodonta (Pyganodon) gibbosa Say

Fig. 2. Altamaha River, "Riverside Park," 4 mi. N of Jesup, Wayne County, Georgia. MCZ 234056. Length 40 mm, height 30 mm, width 22 mm (1⅜ ×).

Fig. 3. Cedar Creek, Fountains Mill, 7 mi. SW of Howkinsville, Pulaski County, Georgia. MCZ 111438. Length 107 mm, height 61 mm, width 48 mm (slightly reduced).

Anodonta (Pyganadon) implicata Say

Fig. 4. *Anodonta newtonensis* Lea. Schuylkill [River], Fairmount [Philadelphia, Philadelphia County, Pennsylvania]. Lectotype USNM 86561. Length 97 mm, height 52 mm, width 39 mm (slightly reduced).

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PLATE 16

Anodonta (Pyganodon) implicata Say

Fig. 1. *Anodonta housatonica* 'Linsley' Gould. Housatonic [River], Corum [= near Huntington, Fairfield County], Connecticut. Holotype USNM 678302. Length 94 mm, height 51 mm, width 34 mm (slightly reduced).

Fig. 2. *Anodonta implicata* Say. Agawam River (outlet of Halfway Pond), Plymouth [Plymouth County], Massachusetts. Neotype MCZ 176769. Length 120 mm, height 60 mm, width 48 mm (somewhat reduced). Interior view, showing the especially distinct pallial line caused by the characteristic anterior-ventral thickening of the shell.

Anodonta (Utterbackia) imbecilis Say

Fig. 3. Magnolia Springs, Perkins, Jenkins County, Georgia. MCZ 234050. Length 90 mm, height 42 mm, width 34 mm (nat. size).

Anodonta (Utterbackia) couperiana Lea

Fig. 4. Pond near Savannah, Chatham County, Georgia. MCZ 119137. Length 87 mm, height 50 mm, width 35 mm (nat. size).

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PLATE 17

Anodonta (Utterbackia) couperiana Lea

Fig. 1. *Anodonta dunlapiana* Lea. [Charleston, Chatham County], South Carolina. Lectotype USNM 86564. Length 83 mm, height 46 mm, width 35 mm (slightly reduced).

Strophitus undulatus (Say)

Fig. 2. Turkey Creek, 8 mi. NW of Edgefield, Edgefield County, South Carolina. MCZ 82807. Length 47 mm, height 29 mm, width 17 mm (nat. size).

Fig. 3. As above. Length 74 mm, height 44 mm, width 27 mm (nat. size).

Carunculina pulla (Conrad)

Fig. 4. *Unio pullus* Conrad. Wateree River, South Carolina. Type lost. (Figures after Conrad). Length 33 mm, height 19 mm, width 13.5 mm (nat. size).

Fig. 5. *Carunculina patrickae* Bates. Savannah River, Johnsons Landing, 10 mi. W of Allendale, Allendale County, South Carolina. Topotype MCZ 255220. Length 32 mm, height 19 mm, width 15.5 mm. Female (1.25 ×). This topotype lacks the sharp posterior ridge of the holotype.

Fig. 6. As above. Length 22 mm, height 13.5 mm, width 10 mm. Male (1.25 ×). This topotype closely resembles Bates' sketch of the allotype.

Fig. 7. University Lake, an impoundment on Morgan Creek, 1 mi. W of Chapel Hill, Orange County, North Carolina. MCZ 261347. Length 25 mm, height 17 mm, width 11 mm. Male (1.25 ×).

Villosa villosa (Wright)

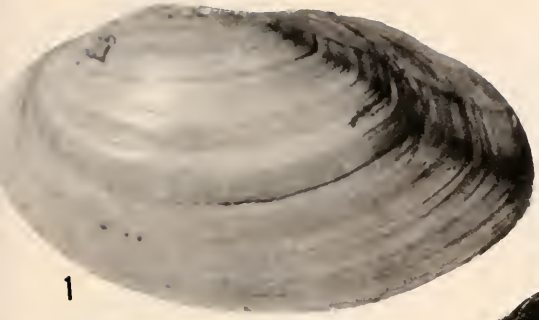
Fig. 8. St. Marys River, Nassau County, Florida. USNM 152066. Length 56 mm, height 29 mm, width 20 mm. Male (slightly reduced).

Fig. 9. *Unio villasus* Wright. Suwannee River [Luraville], Suwannee County, Florida. Lectatype USNM 150503. Length 57 mm, height 28 mm, width 18 mm. Female (slightly reduced).

Villasa vibex (Conrad)

Fig. 10. *Unio vibex* Conrad. Black Warrior River, S of Blount's Spring [Blount County], Alabama. Holotype ANSP 56488a. Length 49 mm, height 28 mm, width 17 mm. Male (approximately nat. size).

Fig. 11. As above. Allotype ANSP 56488. Length 54 mm, height 31 mm, width 19 mm. Female (approximately nat. size).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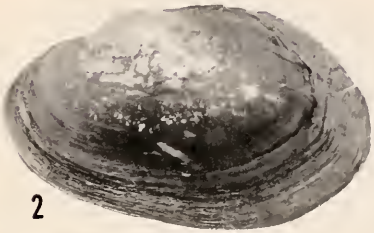
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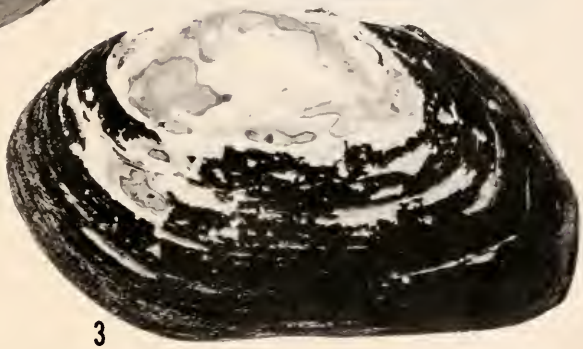
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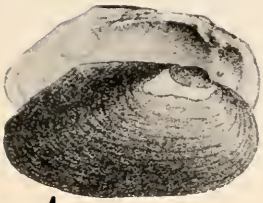
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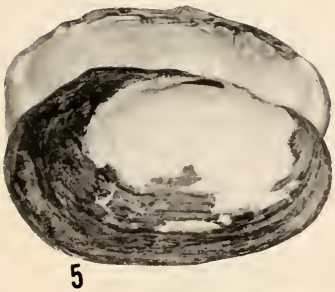
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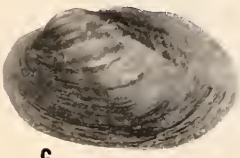
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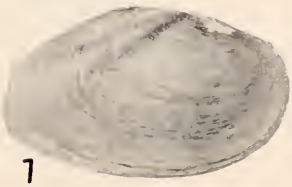
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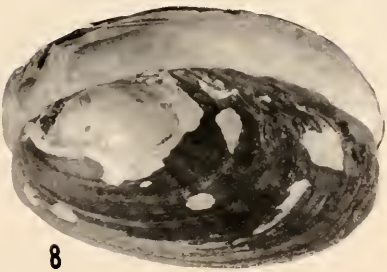
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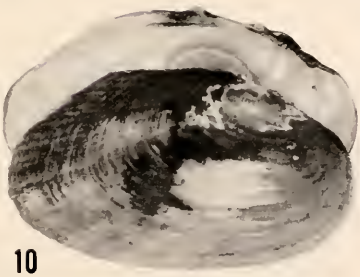
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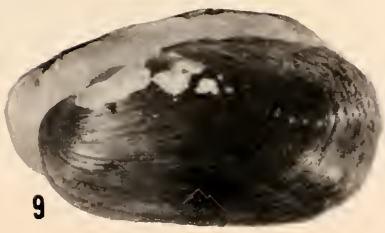
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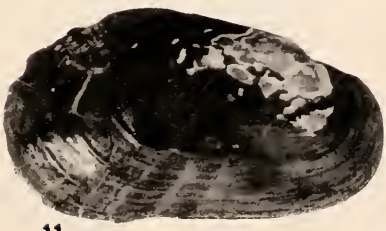
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PLATE 18

Villasa vibex (Conrad)

Fig. 1. *Unio graciliar* Lea. Buckhead Creek [Burke County]; or Tobesaufke [Tobesafkee] Creek, near Macon [Bibb County]; *bath* Georgia. Holotype USNM 85088 [exact locality not indicated]. Length 50 mm, height 28 mm, width 18 mm. Male (slightly reduced).

Fig. 2. *Unio modialiformis* Lea. Santee Canal, South Carolina. Probable holotype USNM 85029. Length 68 mm, height 40 mm, width 25 mm. Female (slightly reduced).

Fig. 3. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 234263. Length 48 mm, height 27 mm, width 17 mm. Male (nat. size).

Villasa delumbis (Conrad)

Fig. 4. *Unio concavus* Lea. Abbeville District [Savannah River drainage], South Carolina. Holotype USNM 85154. Length 55 mm, height 32 mm, width 21 mm. Male (slightly reduced).

Fig. 5. *Unio genuinus* Lea. Bissels Pond, Charlatte [Mecklenburg County], North Carolina. Holotype USNM 85123. Length 52 mm, height 30 mm, width 20 mm. Male (slightly reduced).

Fig. 6. Mill Race, 2 mi. N of Sardis, Burke County, Georgia. MCZ 234340. Length 53 mm, height 30 mm, width 19 mm. Male (nat. size).

Fig. 7. As above. Length 57 mm, height 36 mm, width 19 mm. Female (nat. size).

Fig. 8. *Unio ageecheensis* Conrad. Ogeechee River, Georgia. Lectotype MCZ 146971. Length 64 mm, height 39 mm, width 30 mm. Female (approximately nat. size).

Villasa constricta (Conrad)

Fig. 9. *Unio lienosus constrictus* Conrad. North [= Maury] River, Rockbridge County, Virginia. Lectotype ANSP 56465a. Length 41.4 mm, height 27 mm, width 16 mm. Female (approximately nat. size).

Fig. 10. *Unio genthii* Lea. [Probably from] Deep River, Gulf [Chatham County], North Carolina. Holotype USNM 84834. Length 39 mm, height 27 mm, width 18 mm. Male (nat. size).

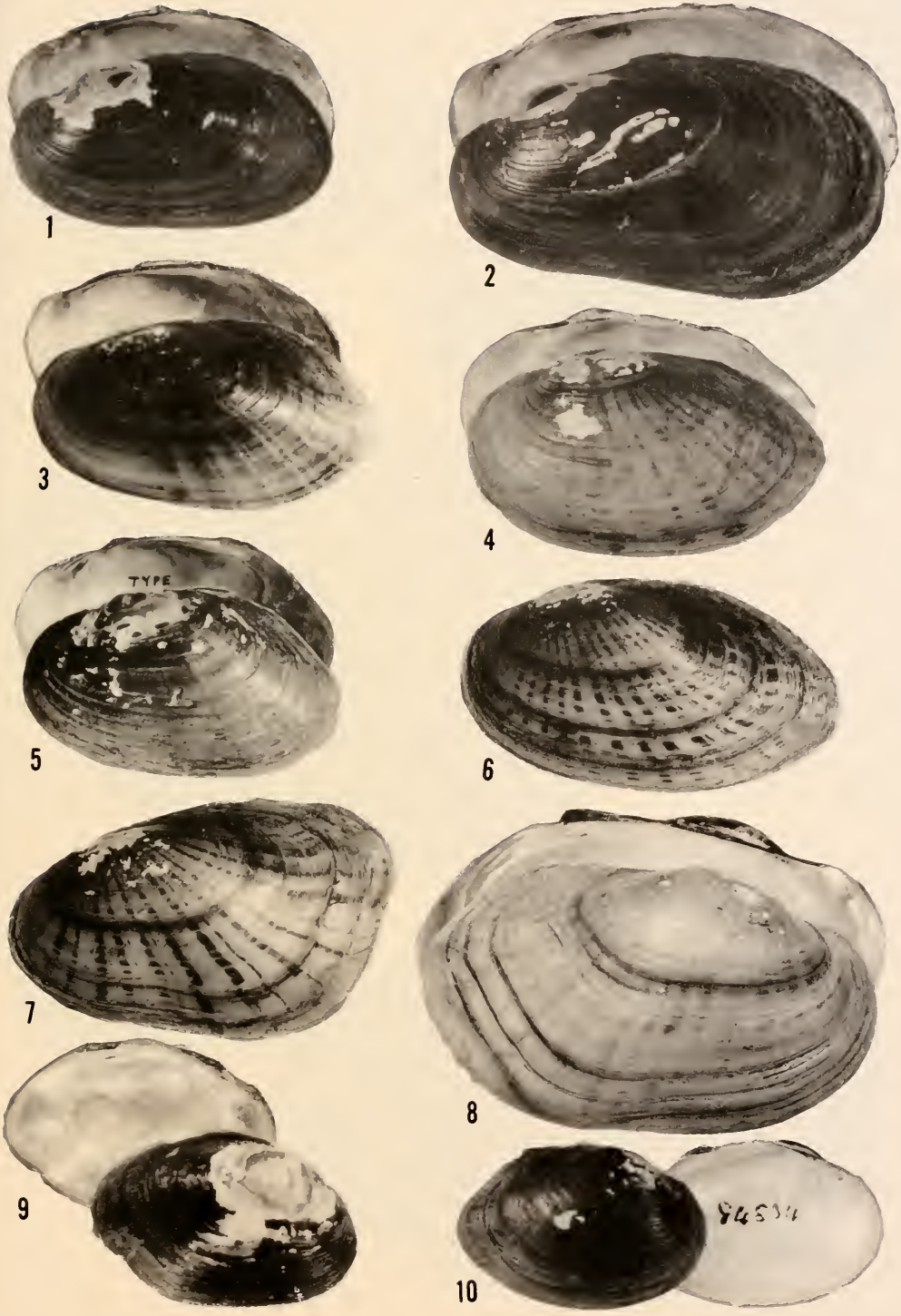
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PLATE 19

Ligumia nasuta (Say)

Fig. 1. Potomac River, Washington, D.C. MCZ 119087. Length 62 mm, height 25 mm, width 12 mm. Male.

Fig. 2. As above. MCZ 5653. Length 66 mm, height 29 mm, width 14 mm. Female.

Lampsilis (*Lampsilis*) *cariosa* (Say)

Fig. 3. Savannah River, 7 mi. NE of Newington, Screven County, Georgia. MCZ 234241. Length 98 mm, height 62 mm, width 42 mm. Male (slightly reduced).

Fig. 4. As above. Length 98 mm, height 69 mm, width 45 mm. Female (slightly reduced).

Fig. 5. *Unio cracatus* Lea. Savannah River, Georgia. Holotype USNM 84908. Length 42 mm, height 27 mm, width 19 mm. Male (slightly reduced).

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PLATE 20

Lampsilis (*Lampsilis*) *dolabraeformis* (Lea)

Fig. 1. Altamaha River, 11 mi. N of Odum, Wayne County, Georgia. MCZ 234197. Length 16 mm, height 12 mm, width 7.5 mm. Male (4×).

Fig. 2. Altamaha River, 10 mi. N of Baxley, Appling County, Georgia. MCZ 234010. Length 91 mm, height 69 mm, width 49 mm. Female (slightly reduced).

Fig. 3. As above. Length 79 mm, height 63 mm, width 50 mm. Male (slightly reduced).

Fig. 4. *Unia dolabraeformis* Lea. Altamaha River, Liberty [now Long] County, Georgia. Holotype USNM 84888. Length 116 mm, height 79 mm, width 51 mm. Male (reduced).

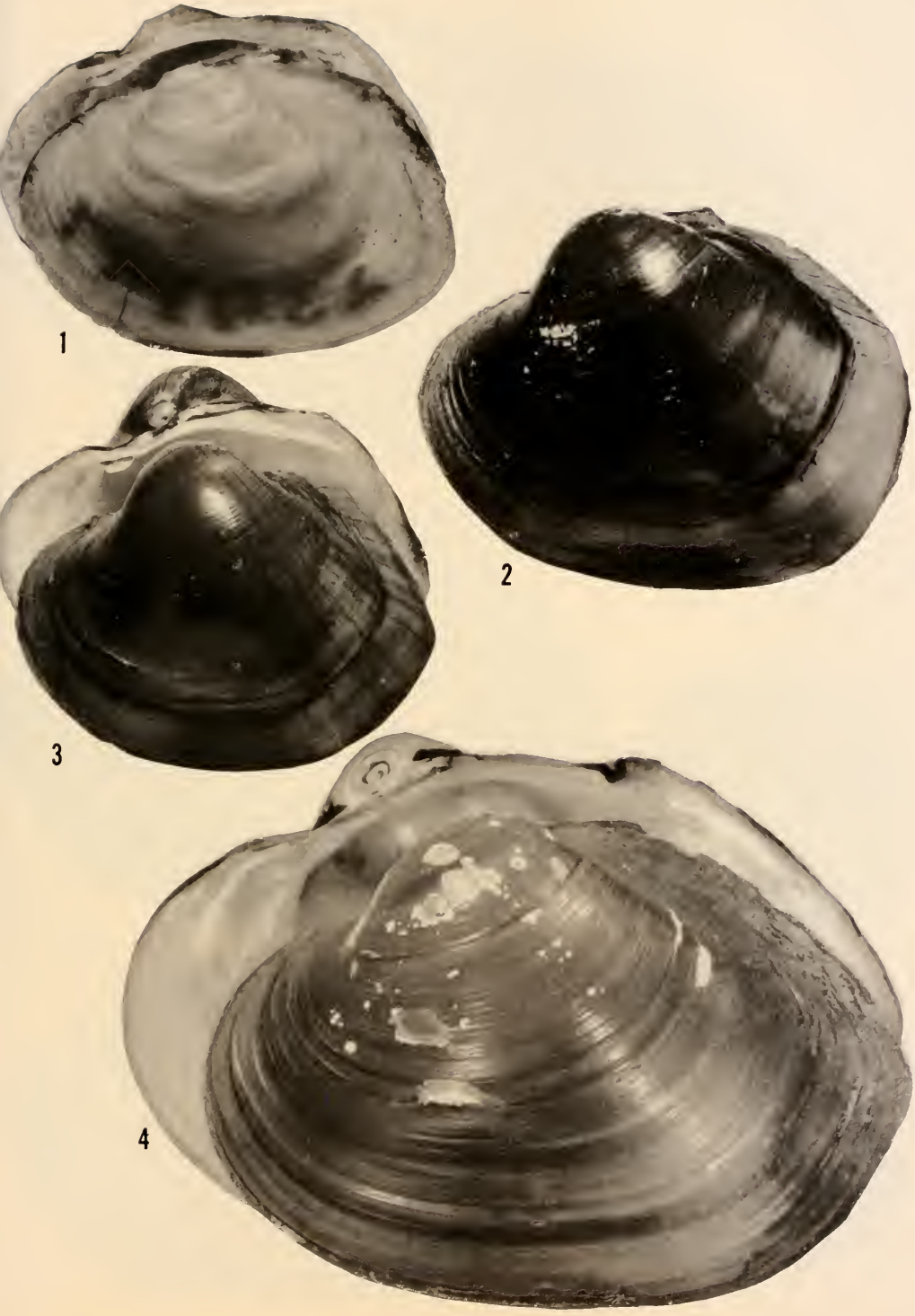
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PLATE 21

Lampsilis (*Lampsilis*) *ovata* (Say)

Fig. 1. *Lampsilis ventricasa cohongaronta* Ortmann. Potomac River, Hancock, Washington County, Maryland. Lectotype Carnegie Museum 61.3999. Length 95 mm, height 60 mm, width 41 mm. Male.

Fig. 2. As above. Allotype Carnegie Museum 61.4000. Length 87 mm, height 62 mm, width 42 mm. Female.

Lampsilis (*Lampsilis*) *achracea* (Say)

Fig. 3. *Unio rosaceus* Conrad. Savannah River, Georgia. Holotype MCZ 178779. Length 73 mm, height 44 mm, width 27 mm. Male (approximately nat. size).

Fig. 4. Lake Waccamaw, [town of] Lake Waccamaw, Columbus County, North Carolina. MCZ 234327. Length 40 mm, height 30 mm, width 17 mm. Female (approximately nat. size).

Fig. 5. As above. Length 50 mm, height 35 mm, width 21 mm. Male (approximately nat. size).

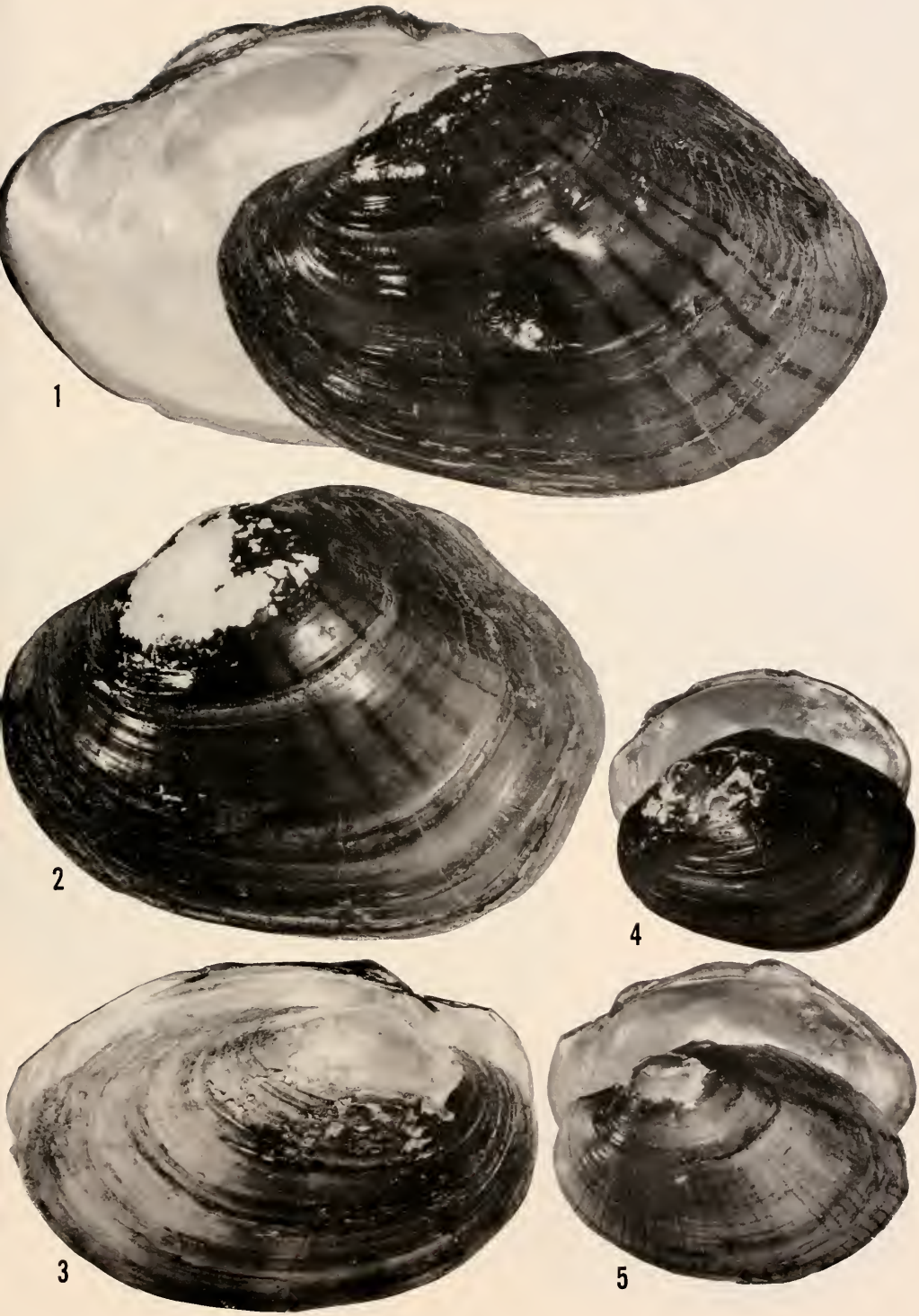
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PLATE 22

Lampsilis (Lampsilis) radiata radiata (Gmelin)

Fig. 1. *Unio conspicuus* Lea. Yadkin River, Salisbury [Rowan County], North Carolina. Holotype USNM 85056. Length 112 mm, height 64 mm, width 39 mm. Male (slightly reduced).

Fig. 2. Greenfield Pond, Wilmington [New Hanover County], North Carolina. USNM 523976. Length 70 mm, height 43 mm, width 28 mm. Male (slightly reduced).

Fig. 3. As above. USNM 452041. Length 76 mm, height 40 mm, width 28 mm. Female (slightly reduced).

Lampsilis (Lampsilis) splendida (Lea)

Fig. 4. Ocmulgee River, 1 mi. S of Lumber City, Telfair County, Georgia. MCZ 234019. Length 71 mm, height 47 mm, width 35 mm. Female (approximately 1.2 ×).

Fig. 5. *Unio splendidus* Lea. Altamaha River [McIntosh or Long County], Georgia. Holotype USNM 84893. Length 70 mm, height 43 mm, width 36 mm. Male (slightly reduced).

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Bulletin OF THE
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Ecological-Behavioral Studies of the Wasps of Jackson Hole, Wyoming

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ECOLOGICAL-BEHAVIORAL STUDIES OF THE WASPS OF JACKSON HOLE, WYOMING

HOWARD E. EVANS

ABSTRACT

During three summers of study, 190 species of wasps (Hymenoptera, Aculeata) were collected in Jackson Hole, Wyoming, principally in six selected sites along the Snake River. The majority of these were fossorial species, about 50 of which were found nesting. For the most part, the species studied appeared to avoid complete competition for prey and for nesting sites, but some possible exceptions are noted. Many species were attacked by parasitic flies, some by cuckoo wasps and other insects. Many of these natural enemies are not host-specific, and maintain high populations at the expense of many different species of wasps. The behavior patterns of the wasps are discussed as mechanisms for (1) avoiding competition with other wasp species, and (2) reducing the success of parasites. Following a general discussion of these subjects, a list of the wasps of Jackson Hole, annotated with ecological and behavioral data, is presented.

CONTENTS

Introduction 451

Study Areas 453

Major Aspects of Ecology 455
- Seasonal cycles 455
- Nesting sites and nest type 455
- Food relationships 457
- Ecological displacement in the species of *Philanthus* 461
- Kinds and specificity of parasites and predators 463
- Summary of interrelationships 466

Behavior Patterns as Adaptations to Life in the Community 468
- Behavior related to competition 468
- Behavior related to parasitism 469
- Summary of behavioral adaptations 472

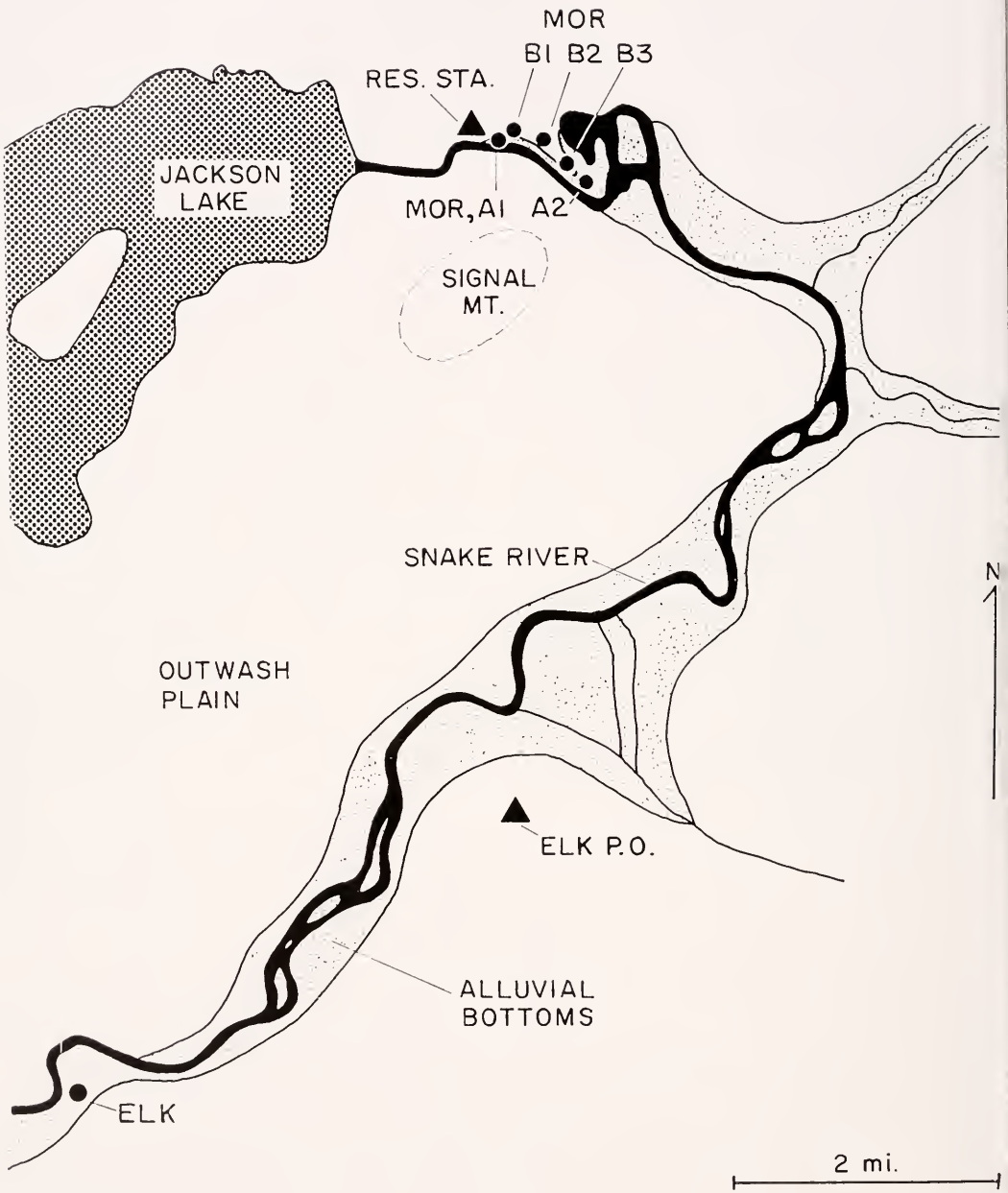
Annotated List of the Wasps of Jackson Hole 474
- Family Dryinidae 475
- Family Chrysididae 475
- Family Sierolomorphidae 477
- Family Tiphiidae 477
- Family Mutillidae 477
- Family Sapygidae 477
- Family Eumenidae 477
- Family Masaridae 479
- Family Vespidae 479
- Family Pompilidae 480

Family Sphecidae 483
- Subfamily Sphecinae 483
- Subfamily Pemphredoninae 486
- Subfamily Astatinae 487
- Subfamily Larrinae 488
- Subfamily Crabroninae 491
- Subfamily Nyssoninae 493
- Subfamily Philanthinae 496

References Cited 502

INTRODUCTION

It was unfortunate that during the flowering of natural history in the 19th century it became fashionable to separate ecology (from *oikos*, home) from ethology (from *ethos*, habits). Surely the habitat and behavior of an animal are all of a piece. Behavior is merely the impingement of an animal upon its environment, while the environment is that portion of the biosphere in which an animal's behavior permits it to thrive. A biotic community is a collection of co-adapted behaviors, no one



Map 1. Sketch of portion of Jackson Hole, Wyoming, showing location of major study areas.

of which is fully understandable of and by itself. That such communities are often enormously complex is troublesome, but this should not divert us from assuming, at least occasionally, a broad view of the interactions of its components. Only such a view can provide insights into the adaptive value and biological significance of observed behaviors; and only behavioral studies can supply insights into the significance of the structures with which systematists are so preoccupied.

Most areas of bare, friable soil in temperate and tropical regions are inhabited by numerous species of digger wasps which often show marked behavioral differences with respect to nesting and hunting behavior. These behavior patterns are stereotyped and relatively easy to observe and to describe. Students have often concluded that the behavioral peculiarities of the various species represent adaptations for avoiding competition with other members of the community, or for reducing the incidence of attacks by the great numbers of parasites which occur in these restricted habitats. There have, however, been few efforts to consider an entire community in the attempt to document these impressions. The present study, although grossly incomplete, represents an effort in that direction.

Jackson Hole, Wyoming, is in many ways ideally suited for studies of this nature. This flat valley surrounded by mountains is relatively high (6750 feet elevation at Moran) and far enough north (about 44° north latitude) so that its insect fauna is more limited in species than that of many more southerly localities. Yet during the brief summer season insects are exceedingly abundant and much more diverse than one might expect, including species of eastern, Pacific coast, and northern distribution, as well as a few Upper Sonoran elements that apparently follow the Snake River drainage, and a few characteristic Rocky Mountain elements. From the point of view of a specialist on digger wasps, the area is especially attractive because much of it is unsuitable for these insects; but those areas which are suitable (i.e., where the soil is friable and more or less devoid of vegetation) contain concentrations of species and individuals perhaps unrivalled anywhere. Another attractive feature is that much of Jackson Hole is part of Grand Teton National Park and thus immune to development or to extensive disturbance. Still another is the presence of the Jackson Hole Research Station at Moran, which provided a pleasant and effective base of operations during three summers of study (1961, 1964, and 1967). I am much indebted to the officers of the station, particularly to its director, Dr. L. Floyd Clarke, for facilitating this research in many ways. I am also indebted to the authorities of Grand Teton National Park for permission to collect specimens for identification.

STUDY AREAS

Most of the floor of Jackson Hole is classified as glacial outwash plain (Fryxell, 1930). East of Jackson Lake much loess has been deposited. This loess not only renders the glacial outwash relatively more friable than elsewhere, but also is the source of much of the alluvial sand which has been deposited here and there on the immediate banks of the Snake River. These studies were conducted partly in areas of "lower outwash plain" and partly in "alluvial bottoms," following Fryxell's terminology (see Map 1). The outwash plains are of Pleistocene origin (Wisconsin glacial stage) and consist chiefly of quartzite gravel with a variable content of loess and a great many cobbles of various sizes; for the most part they are covered with sagebrush (*Artemisia*). The alluvial sand is of recent origin; it is pale in color and of relatively uniform texture. It occurs in low terraces or in bars which often slope into the river, these bars and terraces often

being surrounded by willows and cottonwoods. Groves of lodgepole pine and aspen occur here and there in the outwash plain or adjacent to the alluvial deposits. Where the outwash gravels abut upon the river, the banks are usually high and are constantly being eroded, while the alluvial deposits are several feet lower and in areas of accretion during flooding. In some cases there is a bank separating the margin of the plain from the alluvial bottoms, but more often there is a gradual slope between the two with no sharply marked separation of soil type or cover.

Although I collected wasps at several places in Jackson Hole in an effort to understand the distribution of various species, most of my studies were conducted in three sites near the Research Station. These localities were chosen because of the high concentration of nesting wasps they contained and because each was slightly different as to soil type, vegetation, and composition of the fauna. The three sites are considered below, followed by a description of three additional areas in which extensive collecting was done. In each case I have noted the abbreviation by which these sites are indicated in the text. The three primary localities are shown on Map 1.

(1) Moran, area A (MOR-A). Alluvial sand close beside the Snake River, both near the Station (A1) and at the "Cattle Bridge," about 0.5 miles east of the Station (A2). These are areas of fine-grained, light sand, largely bare but in places partially overgrown with short grass or low herbs. The sand flats are relatively sharply separated from adjacent outwash plain and have a rich and distinctive fauna of digger wasps, including especially species of *Bembix, Oxybelus, Ammophila,* and *Tachysphex.* A2 is shown in more detail in Map 2, and a photograph of a portion of the area is shown in Figure 1.

(2) Moran, area B (MOR-B). Outwash plain between the Station and the Cattle Bridge, especially three areas with very sparse vegetation (B1, 2, 3) which are inhabited by numerous species of wasps including *Philanthus pulcher, P. crabroniformis, Eucerceris* spp., and others (Fig. 2). Certain wasps occupied both the more friable portions of these areas and the more compact soil in the alluvial bars and terraces: such species as *Hoplisoides spilographus* and *Stenodynerus papagorum.* Wasps not largely restricted to either areas A or B are simply labeled "MOR" in the text. Since wasps nesting in A or B generally ranged widely for their prey, the two communities were by no means separate entities. Also, ground squirrels nesting in area B often produced mounds of loosened, friable soil which were occasionally occupied by typical inhabitants of alluvial sand such as *Episyron quinquenotatus.*

(3) Four miles SW of the Elk post office (ELK), roughly seven miles due south of MOR. This area is at a very slightly lower altitude (6650 feet) and is one in which the rather extensive alluvial sand grades almost imperceptibly into glacial outwash, the two soil types intergrading over a low terrace of several acres (Fig. 3). The rich wasp fauna here is dominated by *Bembix americana spinolae* and *Philanthus zebratus nitens.*

(4) Five miles north of the city of Jackson, near the junction of the Gros Ventre and Snake Rivers (JAC). This is at a still lower altitude (6300 feet) and represents an area of extensive alluvial deposits of cobblestones with patches of sand.

(5) Pilgrim Creek (PCR), in Grand Teton National Park and Teton National Forest, some four to seven miles NE of Moran. This is a small stream cutting through forested country, but having numerous sandy deposits along its banks. The sand-inhabiting wasps are similar to those in MOR-A; in addition, there are many twig-nesting wasps here, as is generally true in more wooded areas.

(6) Huckleberry Hot Springs (HHS), in Teton National Forest just north of Grand

Teton National Park and south of Yellowstone. This area is of special interest because of its hot springs, which favor certain species of generally more southerly distribution (e.g., *Bembix amoena*). Studies were conducted in a sandy field adjacent to the major springs.

MAJOR ASPECTS OF ECOLOGY

During the period of study, 190 species of aculeate wasps were collected in these six areas (six other species, listed below in brackets, in peripheral localities). Some species were taken only once or twice and appear to maintain low populations in Jackson Hole, while others were exceedingly abundant in suitable sites. The majority of these wasps (slightly over 100 species) are solitary ground-nesters or are parasites of such wasps. How do so many species of generally similar behavior manage to survive side-by-side during the same brief active season, especially when the presence of so many fossorial wasps permits the build-up of great numbers of parasites? To what extent are the observed behavioral differences among these species understandable in the contexts of interspecies competition and of rampant parasitization? An attempt will be made to answer these questions in this and the next section, leaving the actual documentation to an annotated list of wasps to follow.

I was able to study the nesting and predatory behavior of only about half of the ground-nesters (about 50 species in all), but these were by and large the commoner fossorial species. The majority of the other species have either been studied elsewhere or are closely related to species of known behavior. While most of the conclusions I shall draw here are based on those species studied in detail in Jackson Hole, there is basis for extrapolating them to the remainder of the wasp fauna.

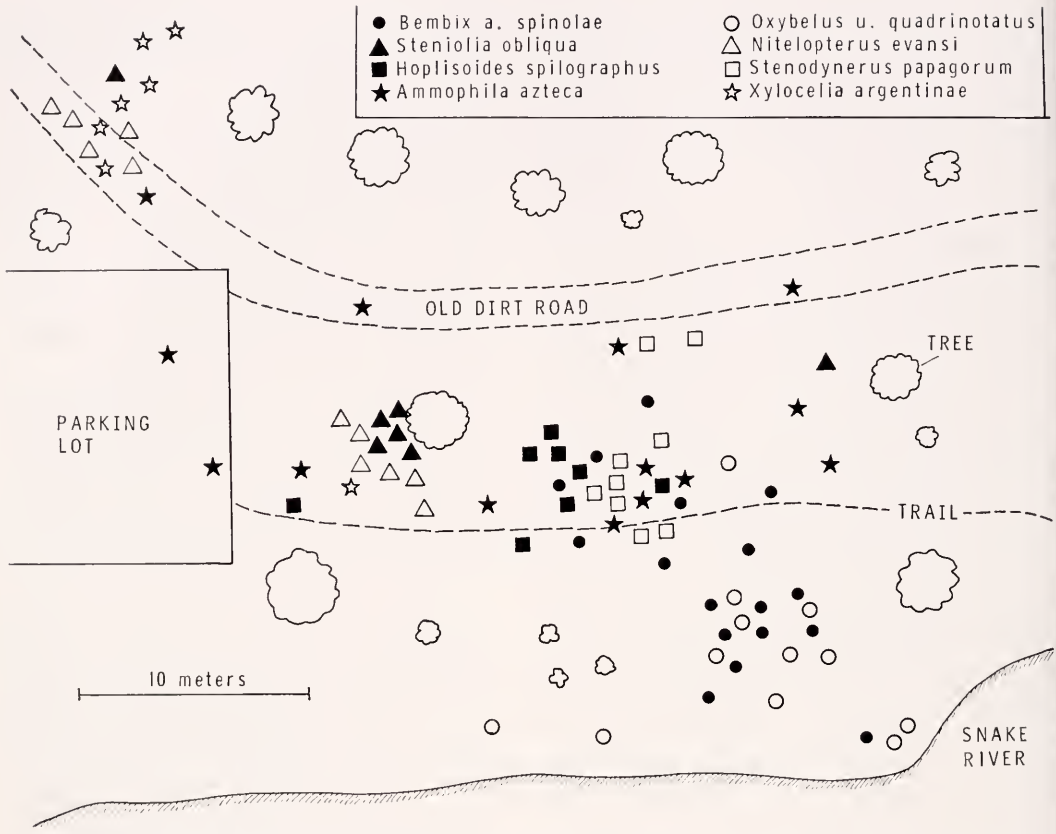
Seasonal Cycles

Since adult female solitary wasps generally live from three to six weeks, it is obvious that to thrive in Jackson Hole they must emerge some time in July in order to have time to complete their nesting cycles before cold temperatures restrict activity in late August or early September. Hence, most species nest more or less simultaneously. Nevertheless some differences in time of emergence and completion of nesting can be noted. For example, *Philanthus pulcher* emerges in late June or early July and has largely disappeared by August first, while *P. pacificus* is a species characteristic of August. Among the spider wasps, *Episyron quinquenotatus* is already active in early July, while *Ageniella blaisdelli* does not appear until about August 1. However, differences in seasonal cycle apparently functioning to reduce competition among species are minimal in this area.

Nesting Sites and Nest Type

Most of the fossorial wasps studied nested in one particular type of soil and no other. *Bembix americana spinolae*, for example, is a gregarious species requiring a fairly large expanse of fine-grained, friable sand; populations of this species occurred only at MOR-A2, ELK, and HHS. The related wasp *Steniolia obliqua*, in contrast, occurs in smaller aggregations in patches of coarser soil, not necessarily entirely bare (although this species is highly gregarious at night and during unfavorable weather, forming massive "sleeping clusters" on vegetation). This species nested at MOR-B3 and on the periphery of A2, in no case forming mixed nesting aggregations with *Bembix*. The differences among the five species of *Philanthus* with respect to soil type are summarized in a subsequent section.

While related wasps in many cases tend to occupy slightly different soil types, any one site often contains a diversity of species belonging to different genera (a widespread phenomenon studied by Elton, 1946). If the soil is of uniform texture, the nests of different wasps may be interspersed, but more often there is some



Map 2. Detailed map of study area MOR-A2, showing location of marked nests of 8 species over a period of several days in late July, 1964. There were many more, unmarked nests of each of these species as well as nests of numerous other species.

tendency for segregation of species in accordance with minor differences in consistency of the soil. Location of nests of some of the species occurring in MOR-A2 are shown in Map 2 (see also Fig. 1). In this community, certain wasps (notably *Bembix* and *Oxybelus*) tended to occupy the very friable sand near the river, certain others occupied more compact sand along trails and roads (especially *Ammophila* and *Stenodynerus*), while still others occupied places in partial shade or with more ground cover (*Steniolia*, *Diodontus*). In this site, the eight species listed on the map all nested in great numbers during late July and early August, along with many other species, some of them nearly or quite as abundant as those listed (e.g., *Episyron quinquenotatus*, *Nitelopterus evansi*, *Podalonia communis*). Thus the scene in midsummer is one of constant activity involving many hundreds of ground-nesting wasps belonging to literally dozens of species.

Moving to a neighboring site of quite different soil type (e.g., to MOR-B3; Fig. 2), one finds a rather different set of wasps, in this case dominated by species of *Philanthus*, *Pisonopsis*, and *Belomicrus*, but with several species in common with A2: *Astata nubecula* and *Steniolia obliqua*, for example. Each of the areas studied had its own particular complex of species, with some overlap in content with other areas;

yet much the same parasites (particularly miltogrammine flies) occurred in all areas in considerable numbers.

Even bare places only a few square meters in extent (such as MOR-B2 and B3) are able to support many fossorial wasps. The nest burrows and entrances are, after all, only a few millimeters in diameter, and each nest is a temporary affair, being permanently closed and abandoned after the completion of provisioning (this is less true of Philanthinae, many of which maintain a single, multicellular nest for their entire lives). Female wasps of the same or different species nesting in close proximity rarely show extensive aggression toward one another; thus, it is possible for many nest-cells to be packed into a limited space. To a certain extent the cells tend to be stratified, for some species make very shallow nests, others relatively deep ones. Nest depth is not necessarily correlated with size of the wasp, for some large species (for example, all species of *Ammophila*) make their nest-cells only a few centimeters beneath the surface. Stratification of nest-cells is well shown in the sandier parts of MOR-A2, where excavations during the inactive season reveal many cocoons of *Bembix americana spinolae* at a depth of about 8 cm (range 5–11 cm) and many of the smaller cocoons of *Oxybelus uniglumis quadrinotatus* at a depth of about 5 cm (range 3–7 cm). An assortment of typical nests from MOR-A2, drawn to the same scale, is shown in Plate V.

While most attention was focused on fossorial species in this study, it should be pointed out that many of the 190 species recorded from Jackson Hole do not nest in the soil but above ground in trees, bushes, or herbs. Some of them nest in hollow twigs (e.g., Eumenidae such as *Ancistrocerus* and *Symmorphus*), others bore in pith or rotten wood (e.g., Sphecidae such as *Ectemnius* and *Pemphredon*), still others build mud nests on stems (*Eumenes*), or on rocks (*Pseudomasaris*), or paper nests in trees, shrubs, or cavities in the soil (Vespidae). It is usually considered that the primitive wasps were fossorial and that various groups have transferred to aerial nesting sites, thus freeing themselves from an attachment to bare, friable soil and from competition with soil-nesters. Competition for hollow twigs is, however, often severe (though not studied here). In the areas of study, twig-nesters were especially prevalent at PCR, which is heavily wooded. Since nesters in the restricted areas of bare soil in Jackson Hole did most of their foraging for prey in surrounding vegetation, and since ground-nesters and aerial-nesters often fed on the nectar of certain flowers side by side, it cannot be said that ground-nesters and aerial-nesters occupied fundamentally different food sites. From the point of view of adult and larval food, they were members of one community, and from the point of view of nesting sites, of two. It should be added that the parasites of aerial-nesters are almost totally different from those of ground-nesters; evidently very different behavioral adaptations are required for exploiting nests in the two situations.

Food Relationships

Collectively, the wasps of Jackson Hole prey upon virtually all kinds of arthropods available in quantities. Yet to a remarkable degree they "divide up" the prey, each species of wasp specializing on one or a few kinds. A general summary of the prey of the commoner fossorial species is presented in List 1, where the wasps are arranged systematically. Consideration of the prey systematically is also instructive. For example, spiders are exploited as prey by at least two species of Sphecidae and by numerous Pompilidae. Yet any one family of spiders is often utilized by only one predator:

Dictynids (Dictynidae) by *Nitelopterus evansi*

Combfooted spiders (Theridiidae) by *Pisonopsis clypeata*
Orbweavers (Araneidae) by *Episyron quinquenotatus*
Crab spiders (Thomisidae) by *Dipogon sayi*
Jumping spiders (Salticidae) by *Pompilus angularis*
Wolf spiders (Lycosidae)
Large *Lycosa* by *Pompilus scelestus*
Medium-sized *Lycosa* by *Cryptocheilus terminatum*
Small lycosids by *Pompilus occidentalis, Anoplius tenebrosus.*

LIST 1

Prey of commoner ground-nesting wasps of Jackson Hole (wasps arranged systematically; see Annotated List, beginning p. 474, for details)

TIPHIIDAE: 3 spp. – Beetle larvae in soil (Coleoptera)

EUMENIDAE
Stenodynerus papagorum – Leaf-mining beetle larvae (Coleoptera)

POMPILIDAE
Cryptocheilus t. terminatum – *Lycosa* spiders (immature) (Araneae)
Episyron q. quinquenotatus – *Araneus* spiders (Araneae)
Pompilus angularis – Small errant spiders, mostly Salticidae (Araneae)
Pompilus scelestus – *Lycosa* spiders (adult) (Araneae)

SPHECIDAE

SPHECINAE
Palmodes carbo – *Cyphoderris* (Gryllacrididae) (Orthoptera)
Palmodes hesperus – *Anabrus* (Tettigoniidae) (Orthoptera)
Podalonia communis – Soil-inhabiting larvae of Noctuidae (Lepidoptera)
Ammophila azteca – Larvae of small moths or of sawflies (Lepidoptera, Hymenoptera)
Ammophila dysmica – Larvae of leaf-feeding Noctuidae (Lepidoptera)
Ammophila macra – Larvae of Sphingidae (Lepidoptera)

PEMPHREDONINAE
Diodontus: 3 spp. – Aphids (Hemiptera)

ASTATINAE
Astata nubecula – Pentatomidae, immature (Hemiptera)
Dryudella montana – Reduviidae, Scutelleridae, Cydnidae (Hemiptera)

LARRINAE
Plenoculus d. davisi – Miridae, adult and immature (Hemiptera)
Solierella affinis – Nabidae, immature (Hemiptera)
Nitelopterus evansi – *Dictyna* spiders (Araneae)
Pisonopsis clypeata – Theridiid spiders (Araneae)
Tachysphex: 5 spp. – Acridid grasshoppers, immature (Orthoptera)

CRABRONINAE
Lindenius columbianus – Small parasitic wasps, flies, and bugs (Hymenoptera, Diptera, Hemiptera)
Crossocerus maculiclypeus – Very small flies (Diptera)
Belomicrus f. forbesii – Miridae (Hemiptera)
Oxybelus uniglumis quadrinotatus – Diverse small flies (Diptera)

NYSSONINAE
Gorytes canaliculatus asperatus – *Idiocerus* leafhoppers (Hemiptera)
Hoplisoides spilographus – Immature treehoppers, Membracidae (Hemiptera)
Stictiella emarginata – Adult moths, Noctuidae (Lepidoptera)
Steniolia obliqua – Beeflies, Bombyliidae (Diptera)
Bembix americana spinolae – Diverse, medium-sized flies (Diptera)

PHILANTHINAE
Aphilanthops subfrigidus – Queen *Formica* ants (Hymenoptera)

Philanthus: 5 spp. – Bees and wasps (Hymenoptera)
Eucerceris flavocincta – Adult, medium-sized weevils (Coleoptera)
Eucerceris fulvipes – Adult, very small weevils (Coleoptera)

In some cases this specialization in predation is absolute; for example, there are now literally hundreds of records from many areas which indicate that *Episyron quinquenotatus* takes only orbweavers. In other cases there is overlap which is more apparent than real: *Pisonopsis clypeata*, for example, takes an occasional orbweaver, but only small species occurring close to the ground and not utilized by *Episyron*. Inclusion of other, less common Pompilidae in this listing would complicate the picture, but by no means smudge it completely. Two species of *Aporinellus*, for example, prey upon Salticidae, but these are very small wasps and undoubtedly take smaller spiders than *Pompilus angularis*. A number of small Pompilidae besides those listed are known to employ small lycosids, e.g., *Anoplius ithaca*, *A. imbellis*, *Priocnemis notha*, and some of these use errant spiders of other families as well. It is probable that *Cryptocheilus* utilizes immature *Lycosas* which, when mature, might serve as prey for *Pompilus scelestus*. Thus, there would appear to be competition for prey among the numerous predators on errant spiders. Two points should be made here: (1) these are abundant spiders, readily available and not requiring highly specialized hunting behavior; and (2) the wasps involved are parasitized by certain Pompilidae (*Ceropales*, *Evagetes*) and by miltogrammine flies, and their populations may thus be suboptimal. I would assume that most pompilids, like many other insects, occur at relatively low densities as a result of parasite pressure and thus are able to occupy similar or even identical food niches. In any case, the pompilids in question have different nesting behaviors and often occupy different nesting sites; thus, they are by no means ecological homologues. For example, of the two predators on small lycosids listed, *Pompilus occidentalis* nests primarily in wooded areas, *Anoplius tenebrosus* in open country.

Examination of the predators on major groups of insects reveals situations similar to that prevailing among the spider-hunters. The fauna of Jackson Hole includes quite a number of predators on Orthoptera. Two species of *Palmodes* take large long-horned grasshoppers; present records indicate that they use different species, but this may not hold up. *Larropsis capax* is known to utilize camel crickets (*Ceuthophilus*). Five species of *Tachysphex* use immature short-horned grasshoppers (Acrididae), but these species are not all the same size. Furthermore, the larger species use one grasshopper per cell, hence, they take grasshoppers slightly larger than themselves, while the smaller species use several per cell and generally use grasshoppers smaller than themselves. Hence, the spread in size of prey is greater than that in size of the wasp. The following is a list of the species of *Tachysphex*, giving the mean length of the females and the mean length of the grasshoppers utilized (in the case of *aethiops* and *nigrior* only one prey each was taken; see Annotated List for data).

Species of *Tachysphex*	Mean length of females	Mean length of prey
aethiops	13.0 mm	16.0 mm
tarsatus	9.5 mm	10.0 mm
nigrior	9.0 mm	9.5 mm
terminatus	7.5 mm	6.5 mm
sp. nr. linsleyi	6.5 mm	6.0 mm

Since these species nest more or less simultaneously, and since each species of grasshopper tends to be at one growth stage at this season, it is unlikely that the species of *Tachysphex* at the ends of this spectrum often use the same species of prey. However, by presenting only the means I have concealed the fact that each species takes grasshoppers over a considerable size range (see especially Kurczewski, 1966). Undoubtedly considerable overlap

in prey does occur, and much the same reasoning may apply as in the case of the spider-hunters.

The predators on Coleoptera seem to show little overlap in prey preferences. *Eucerceris flavocincta* is a large wasp using rather large weevils, *E. fulvipes* a smaller wasp using very small weevils. Leaf-mining larvae of weevils and leaf beetles are employed by *Stenodynerus papagorum*, and it is probable that here as elsewhere twig-nesters of the genera *Symmorphus* and *Leptochilus* utilize beetle larvae feeding externally on leaves. The species of *Tiphia* presumably attack the subterranean larvae of scarab beetles here as elsewhere, and *Methocha* the larvae of tiger beetles.

Quite a number of wasps in Jackson Hole employ Lepidoptera as prey. Of the two that are known to employ adult moths (though not actually studied here), *Stictiella emarginata* uses Noctuidae, the twig-nester *Lestica interrupta* small Microlepidoptera. Species employing lepidopterous larvae include especially several *Podalonia* (using subterranean larvae or "cutworms") and several *Ammophila* (using external leaf feeders). Among the *Ammophila*, *macra* uses very large sphingid larvae, *dysmica* medium-sized Noctuidae, *azteca* small larvae of Geometridae and other groups, including sawflies, and *pilosa* uses principally larvae of lycaenid butterflies. Five other less common species of *Ammophila*, unstudied in this area, may well show some prey overlap with these species. Many aerial nesters also utilize lepidopterous larvae. *Ancistrocerus catskill*, for example, is common in Jackson Hole; this species uses small Microlepidoptera and thus may not compete seriously with any of the ground-nesters. Some of the other Eumenidae may, however, do so.

In the case of the several predators on Diptera nesting in the ground, some slight overlap in prey is apparent between *Steniolia obliqua* and *Bembix americana spinolae* and between the latter species and *Oxybelus uniglumis quadrinotatus*; *Crossocerus maculiclypeus* utilizes extremely small flies not otherwise employed by any ground-nesters studied. There are major gaps in knowledge here, as species of *Crabro* (ground-nesters) and *Ectemnius* (nesters in wood) were common in Jackson Hole and are predators on Diptera: however, I obtained no prey records and thus cannot compare them directly with the species studied.

In the case of predators on true bugs (Hemiptera), it should be pointed out that *Astata nubecula* preys on fairly large stinkbugs, *Dryudella montana* on small, immature bugs of several related families, *Plenoculus davisi* and *Belomicrus forbesi* on plant bugs (Miridae) (but so far as known on different species). Other Hemiptera-predators attack treehoppers (*Hoplisoides*), leafhoppers (*Gorytes* and presumably *Dienoplus*, *Mimesa*, *Crossocerus wickhamii*, and the Dryinidae), and aphids (various Pemphredoninae, including three species of *Diodontus*). Leafhoppers and aphids are exceedingly abundant insects, and it is not surprising that they are attacked by a variety of wasps. None were studied in sufficient detail to determine how much prey overlap occurred, but it can confidently be said that the wasps involved are diverse in habitat and nest type. For example, two of the three species of *Diodontus* were common, yet one was confined to friable, flat sand at MOR-A2, the other to roadside banks of coarse glacial outwash at MOR-B3.

Rather than prolong this discussion, I should like to consider one other group in greater detail: the species of *Philanthus*, predators on wasps and bees, and among the most abundant wasps in Jackson Hole. These exhibit ecological displacement in an unusually striking manner and also serve to point up the great complexity of communities such as this, for several species utilize as prey fossorial wasps nesting close to them, while some utilize the parasites of wasps or of their prey.

Ecological Displacement in the Species of Philanthus[1]

Despite the abundance of members of this genus in Jackson Hole, it is an unusual experience to encounter more than one species at one time and place. At MOR-B, *P. pulcher* is a dominant species through July, each female making a series of rather shallow nests (Fig. 36) in bare places relatively free of stones; during three summers, I have never collected or seen this species after August 3. *P. crabroniformis* is an equally abundant species, making its first appearance about July 22, but beginning to nest in numbers a week or so later. On a few occasions I have seen *crabroniformis* females digging in sites occupied by *pulcher*, but for the most part they select places where the soil is notably harder and stonier. Since wasps of this species make relatively deep, complex nests which they usually occupy for life, and since all expansion of the nest is at lower soil strata (Fig. 38), friability of the surface soil is evidently less critical. Mean cell depth of *pulcher* is 8.3 cm (range 6–10 cm), while that of *crabroniformis* is 13 cm (range 9–21 cm). *P. pulcher* preys upon bees and wasps in approximately equal numbers, including such diverse forms as cuckoo wasps, leaf-cutter bees, and several parasitic bees (List 6). Most of these are small insects, but a few are about as large as *P. pulcher*; the mean length of females of this species is 10 mm, the mean length of the prey 6 mm (range 4–11 mm).[2]

P. crabroniformis, on the other hand, although averaging slightly larger than *pulcher*, uses a great many halictid bees much smaller than itself; only occasionally does this species employ wasps as prey (List 7). The mean length of female *crabroniformis* is 11.5 mm, that of the prey only 5.5 mm (range 4–8 mm). One species of wasp and six species of bees appear on both lists of prey; 15 per cent of the species utilized by *pulcher* were also utilized by *crabroniformis*, but these make up about one third of the records for *pulcher* (species of *Dialictus* being the most commonly used prey of both species). Thus there is a fair amount of overlap in prey, the larger species curiously tending toward smaller prey than the smaller. However, the two species displace one another almost completely with respect to soil type and stratum and with respect to nesting season. In the final analysis, they may be characterized as non-competitors.

A third species, *P. pacificus*, appears in late July, at about the same time as *crabroniformis*. It is a considerably smaller species (mean length of females about 9 mm), yet a comparison of available prey records reveals that the two compete for much the same bees and wasps (mean length of prey of *pacificus*: 5.2 mm, range 4–7 mm). Both use only an occasional small wasp, but use ground-nesting bees in great numbers, small Halictidae making up 78 per cent of the prey of *pacificus*, and 96 per cent of the prey of *crabroniformis*. The majority of species taken as prey by *pacificus* (List 9) also appear on the list for *crabroniformis*. Evidently these bees are sufficiently abundant in August to support aggregations of two species of *Philanthus*. However, these two wasps exhibit a total separation in nesting sites, *pacificus* being confined to fine-grained,

[1] I use the word "displacement" to refer to different ways of exploiting the habitat, not in the sense of physical displacement of one species by another. That is, a species occurring in a particular area and habitat will have features which are displaced by other features in related species also occurring there. Darwin (1859) spoke of this as "divergence of character" and stressed that "more living beings can be supported in the same area the more they diverge in structure, habits, and constitution" (Mayr, 1963).

[2] Length of the prey is a poor measurement of size, since bees and some wasps are notably broader and heavier than such wasps as *Mimesa*, *Ammophila*, etc. However, it was the only convenient measurement I could make with the available time and facilities.

light sand in bars close beside the river (at MOR-A2) or in the center of sandy roads near the river (at ELK). In no case did I find these two species nesting within 200 meters of one another. Like most *Philanthus*, they probably do most of their hunting on flowers (taking many more male bees than females), and it is probable that they exploit different patches of *Solidago* and other flowers, at least for the most part.

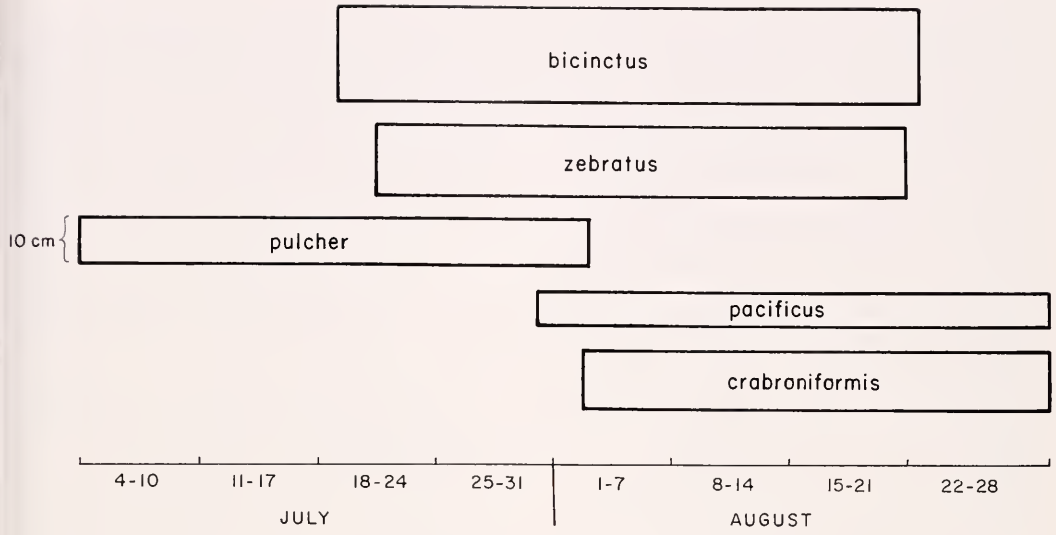
A fourth species of *Philanthus*, *zebratus nitens* (referred to hereafter simply as *zebratus*), appears in mid-July and is active until mid-August. This is a large, colorful species which nested in large numbers in moderately friable sandy soil at ELK and also along a sandy road at HHS; I did not take the species at MOR at any time. At ELK, *zebratus* occupied more hard-packed sand than *pacificus*, and at HHS more friable sand than *crabroniformis*. I would characterize this species as preferring a soil type intermediate between those two species, and the absence of a suitable expanse of such soil at MOR may explain its absence there. In any case, *zebratus* exhibits almost no prey overlap with either of those species, since it uses notably larger prey. The mean length of female *zebratus* is about 14 mm, the mean length of the recorded prey 11.3 mm (range 8–18 mm). This figure is somewhat deceptive, since the longer prey consisted of Ichneumonidae and such Sphecidae as *Ammophila*, which are very slender-bodied. Nevertheless, *zebratus* does clearly occupy a different food-size niche than *pacificus* and *crabroniformis*; no species and only one genus appear in common on the lists for *pacificus* and *zebratus* (List 8), and only one species and two genera in common on the lists for *crabroniformis* and *zebratus*. As a predator, *zebratus* has much more in common with *pulcher*, since it uses wasps and bees in about equal numbers and uses prey averaging only slightly smaller than itself. The prey lists for these two species have five genera (no spp.) of wasps and eight genera (3 spp.) of bees in common. However, I found the two species nesting in the same situation only once (at ELK) and then on a date (July 10) when only *pulcher* was nesting.

The fifth species of *Philanthus* occurring in Jackson Hole, *bicinctus*, I shall discuss only briefly, since I encountered it only occasionally, and since Armitage (1965) has discussed a nesting aggregation at the South Gate of Yellowstone. This species makes very deep nests in thinly vegetated slopes where the soil is very coarse and stony; the prey consists principally of bumblebees of several species, rarely of other large bees. Thus it is isolated from the other four species both with respect to habitat and with respect to prey.

Differences among the five species in seasonal cycle and size of the females are summarized in Text-figure 1; however, it should be remembered that size of the wasp is not a wholly dependable reflection of size of the prey, for *crabroniformis* uses prey averaging smaller than *pulcher*. Also, the figure makes no attempt to indicate differences in soil type utilized for nesting, which (although characterized here only subjectively) is evidently at least slightly different in each of the five species, and quite conspicuously different in some cases (e.g., *pacificus* vs. *crabroniformis*). Some of the several conspicuous behavioral differences between the five species evidently serve to sustain the almost complete ecological displacement among these species. Others probably serve to maintain reasonably high population sizes in spite of the presence of an abundance of parasites. It will be more profitable to explore this subject after surveying the parasites briefly.

Kinds and Specificity of Parasites and Predators

The approximately 100 species of ground-nesting wasps occurring in the areas of study were attacked by a consider-



Text-figure 1. Comparison of the five species of *Philanthus* occurring in Jackson Hole with respect to mean size of females (width of bars) and period during which females provision their nests.

able array of parasites and predators[1]; 25 species of Diptera and Hymenoptera were either actually shown to attack these wasps, or can be assumed to attack them with a high degree of probability. Some of these are relatively host-specific, attacking one or a few related species of wasps, while others show little or no specificity, attacking ground-nesters of many diverse species. Specificity implies a measure of coevolution of host and parasite; that is, the two may acquire behavioral traits that permit them to coexist without marked population depressions. On the other hand, non-specific parasites may have varying success depending upon the behavior of their host, which cannot usually have evolved behavior patterns fitted to reducing the success of all of its various attackers. Thus, non-host-specific parasites and predators may be more significant in producing population crashes in certain hosts ill-adapted to them and in bringing about rapid but narrowly adaptive changes in nesting behavior.

Good examples of host-specific parasites are provided by members of the cuckoo-wasp genus *Parnopes*, several species of which have a wide distribution but are seldom abundant, perhaps because the sand wasps they attack have evolved nest closures sufficient to delay or prevent entry by the female parasites. In Jackson Hole, *P. edwardsii* is a parasitoid of *Steniolia obliqua* and probably of *Bembix americana spinolae* and *B. amoena*, the female digging through the nest closure to oviposit on the larva (Evans, 1966a). Chrysidids of the genera *Hedychrum*, *Hedychridium*, and *Ceratochrysis* were also found associated with certain ground-nesters (see Annotated List below), but the degree of host-specificity is not known.

[1] In fact, all of these are predators as that word is most commonly used. Like many entomologists, I use the word "parasite" loosely and here apply it to two kinds of associations: (1) parasitoids, which feed upon the host slowly and destroy it as they reach maturity; and (2) cleptoparasites, which feed principally upon the prey in the cell, but usually also kill the host larva. "Predators," as I use the word here, are also of two kinds: (1) those that capture and feed directly upon the prey, e.g., asilid flies; and (2) those that capture and paralyze prey and take it to the nest as food for the larvae, e.g., digger wasps.

The species of *Bembix* are also attacked by two apparently host-specific dipterous parasites: *Physocephala texana*, a conopid fly attacking the adults, and *Exoprosopa dorcadion*, a bee-fly that oviposits in open holes, its larva attacking the wasp larva. *Hoplisoides spilographus* and probably the species of *Gorytes* and *Dienoplus* are attacked by wasps of the genus *Nysson*, while various spider wasps are attacked by members of the cleptoparasitic pompilid genera *Ceropales* and *Evagetes*. (Records will be found in the Annotated List; for further details on these and related species see Evans and Yoshimoto, 1962, and Evans, 1966a.) This essentially completes the list of parasites that confine their attacks to a restricted group of hosts in this area. None of them are overly abundant in Jackson Hole, and there is no evidence from here or elsewhere that they cause profound depressions in the population sizes of their hosts.

Some of the non-host-specific parasites, notably the miltogrammine flies (Sarcophagidae), stand in strong contrast to these. These flies are abundant in virtually all areas inhabited by ground-nesting wasps in Jackson Hole as elsewhere. The most ubiquitous species is *Senotainia trilineata* (Fig. 10), often spoken of as a "satellite fly," since the females follow closely behind prey-laden wasps and larviposit upon the prey, often just as it is being taken into the nest. The small maggots typically destroy the egg of the wasp within a few hours after it is laid, then develop at the expense of the prey in the cell. Generally several maggots are deposited at once, and several (rarely up to 20) may develop successfully in one cell. In Jackson Hole, I have reared this fly from the cells of six species of Sphecidae, and altogether 17 species belonging to three families may be regarded as probable hosts (List 2). In fact, records from many localities suggest that these satellite flies follow wasps of many genera of several families and that their larvae develop successfully in the nests of most species. However, in the case of maggots introduced by progressive-provisioners (such as *Bembix*) after the larva has begun to grow, the wasp larva and the maggots may both survive; I record one such case for *B. americana spinolae* and *Senotainia trilineata* below.

LIST 2

Hosts of *Senotainia trilineata* at Jackson Hole[1]

EUMENIDAE
Stenodynerus p. papagorum (Viereck)*

POMPILIDAE
Episyron q. quinquenotatus (Say)**

SPHECIDAE
Aphilanthops subfrigidus Dunning*
Astata nubecula Cresson
Belomicrus f. forbesii (Robertson)
Bembix americana spinolae Lepeletier
Gorytes canaliculatus asperatus Fox*
Nitelopterus evansi Krombein*
Oxybelus uniglumis quadrinotatus Say
Philanthus crabroniformis Smith
Philanthus pacificus Cresson*
Philanthus pulcher Dalla Torre*
Philanthus zebratus nitens (Banks)
Plenoculus davisi Fox**
Tachysphex nigrior Fox*
Tachysphex tarsatus (Say)**
Tachysphex terminatus (Smith)**

Two other satellite flies, *Hilarella hilarella* and *Taxigramma heteroneura*, were taken at MOR, the first associated with three unrelated species of Sphecidae, the second with two unrelated sphecids. I did not rear these flies from any nests and little is known of their biology, but I would assume that they are similar to *Senotainia*

[1] Reared from nests unless marked with an asterisk:
* Seen following females but not reared from cells;
** Known to be attacked on basis of studies elsewhere.

in their mode of attack and development, as well as in their lack of host-specificity.

The miltogrammine fly *Metopia argyrocephala* was reared from a nest of *Gorytes canaliculatus asperatus* and was found closely associated with the nests of five other sphecids. This fly also sometimes follows female wasps to their nests, but rather than larvipositing on the prey in transit, it enters the nest and larviposits in the cell. "Hole-searchers" such as this probably also locate open nests by random searching.

One of the most abundant Miltogramminae in Jackson Hole is *Phrosinella pilosifrons*, a relatively large fly with slightly expanded front tarsi that is often seen digging at closed nest entrances (Fig. 14). I have never observed this fly trailing female wasps or being attracted to open holes; rather it moves from one closed nest entrance to another where it now and then attempts to dig through the closure, when successful presumably larvipositing in the burrow or cell. Whether it is attracted to nests by the sight of fresh digging or by odor has not been determined. The maggots of *Phrosinella* are large, and usually one develops per nest cell (in a rearing tin one maggot may move to other cells and destroy them). In Jackson Hole, I found this species associated only with the species of *Philanthus*, and reared numerous flies from the cells of three species: *pulcher*, *crabroniformis*, and *zebratus*. However, other species of *Phrosinella* are known to attack a diversity of ground-nesters that maintain closures, and I would expect the same to be true of *pilosifrons*.

There is need for detailed field studies of these and other species of Miltogramminae, for these flies are unquestionably major pests of digger wasps and may have played an important role in molding various attributes of their nesting behavior, as discussed below. Despite various devious flight patterns, closures, accessory burrows, and so forth, the percentage of cells successfully attacked may be quite high: about 20 per cent in *Philanthus zebratus nitens*, a species possessing several behavioral mechanisms evidently functioning to reduce the success of parasites. There is evidence that these flies sometimes cause marked decline in local populations of certain digger wasps.

Among the general predators at Jackson Hole should be mentioned asilid flies, including at least two species of *Laphria*, which tend to prey extensively upon Hymenoptera. These flies were often seen perching on logs or bushes overlooking nesting sites and dashing periodically at flying insects; one was taken with a sphecid wasp in its grasp, while others were seen with bees and sawflies. Spiders of many kinds also occur on the ground and in vegetation and probably take a considerable toll among the small wasps, although I obtained only one specific record of predation by a spider.

Finally, it should be remembered that four species of *Philanthus* prey upon wasps, two of them quite extensively. While the majority of wasps taken as prey are males, a good many females are also taken, including species nesting in close proximity to *Philanthus* (Lists 4 and 7). It is interesting to note that while Sphecidae, Eumenidae, Masaridae, Chrysididae, and even parasitic Hymenoptera appear on the lists of *Philanthus* prey, Pompilidae do not. Pompilids are certainly abundant at Jackson Hole both on the ground and on various flowers visited by *Philanthus*. Possibly their swift and erratic flight patterns render them difficult to capture. It should also be noted that in no case has a *Philanthus* been found to take another *Philanthus* (of any species) as prey, even though *zebratus* has been found to use the very similar and closely related wasp *Aphilanthops subfrigidus*. Although Rathmayer (1962) has shown that *Philanthus* is immune to its own venom, it seems more probable that these wasps are able to avoid attacking members of their own genus, perhaps by olfactory cues. This would be

an exciting problem to study experimentally.

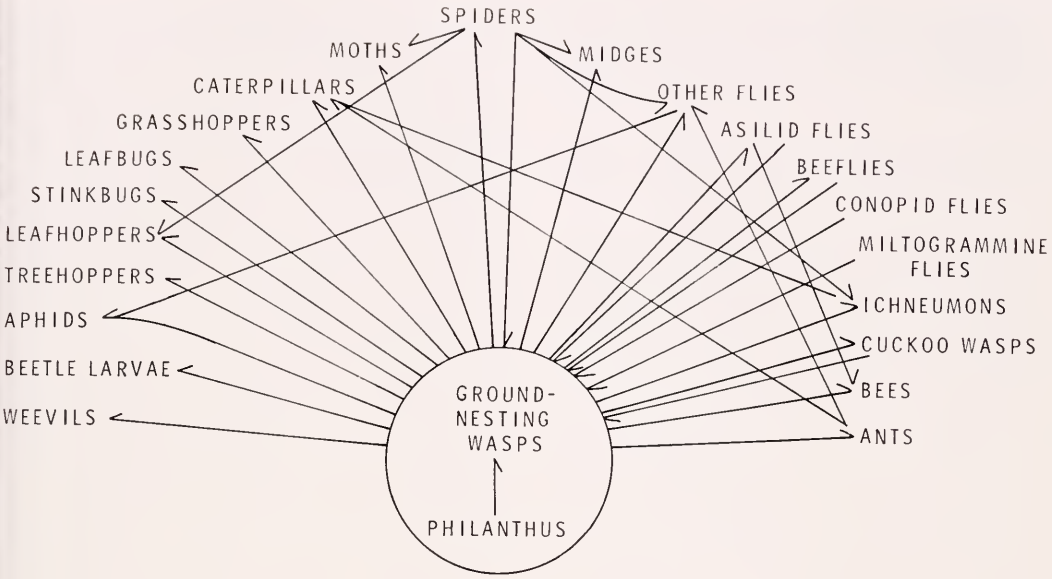
Summary of Interrelationships

Digger wasp communities of Jackson Hole involve food webs that cannot adequately be summarized because of their complexity and because of shortcomings in our knowledge. The wasps are energetic predators that harvest great numbers of arthropods within and around their nesting sites. For example, if there were 50 nesting female *Bembix americana spinolae* at MOR-A2 and each prepared five nests containing 20 flies each (all highly conservative estimates), these wasps would have collected 5000 flies from the surrounding countryside. The aggregation of *Philanthus zebratus* at ELK contained an estimated 200 females, each of which prepared an estimated 15 cells provisioned with an average of about six prey; thus the members of this population must have collected at least 18,000 bees and wasps, evidently chiefly from flowers in the general vicinity of the nesting area.

Considering the abundance of ground-nesting wasps in certain areas and their efficiency as predators, it is not surprising that most species occupy different food niches. That some species do appear to prey upon the same arthropods during the same season may be attributable to: (1) the great abundance of such insects as aphids, leafhoppers, small halictid bees, etc.; and (2) the fact that virtually all wasps may maintain submaximal population sizes as a result of widespread parasitization, especially by miltogrammine flies. During seasons when, for climatic or other reasons, certain arthropods are unusually scarce, wasps which occupy similar food niches may be especially affected, and during seasons when one particular non-specific parasite is especially abundant, those species relatively unprotected against it may suffer profound population declines. Various short-range and long-range climatic factors may affect predators, prey, and parasites differently, thus providing a continually changing environment which must be met by behavioral adjustments of one kind or another, or decline and local extinction may follow.

Some of these changes were obvious during the three summers I worked in Jackson Hole. In 1964, deerflies (*Chrysops*) were exceedingly abundant at MOR, and these flies were used as prey by *Bembix* almost to the exclusion of other flies. In 1967, doubtless as a result of a different rainfall or temperature pattern, deerflies were rarely in evidence, and the *Bembix* had shifted wholly to other flies (List 3). Some of these other flies provide the common prey of *Oxybelus* and of *Steniolia obliqua*. The latter species underwent a steady decline in numbers at MOR from 1961 to 1967. To what extent this has been due to competition for prey with *Bembix*, to success of its several parasites, or to changing climatic factors, is unknown. Since *Steniolia* often nests in the middle of paths and dirt roads, its decline may be largely the result of increasing numbers of humans and horses. Human interference may, in fact, be having an important influence on wasp populations even in this supposedly sacrosanct area. I suspect, for example, that construction of the Jackson Lake dam and resulting control of flooding along the Snake River may eventually diminish the alluvial deposits along the river. Sand bars have their own life cycles, and unless refreshened by wind or water eventually become overgrown and the soil greatly altered.

Even in the absence of human interference, changes in soil conditions and in vegetative cover are continually occurring, and these changes result in the expansion and contraction of suitable nesting space for certain species. It is difficult to evaluate such factors, as little is known of the precise edaphic relationships of wasp species. As in the case of food resources, it is probable that the abundance of natural



Text-figure 2. Diagrammatic representation of some of food relationships of wasps and their prey and parasites at Jackson Hole. Direction of arrow indicates direction of predatory or parasitic relationship (for energy flow, read arrows backward).

enemies ameliorates the intensity of competition for space; that is, many populations may be kept at levels sufficiently low that they do not fill all suitable nesting areas. At the same time, the need for bare, friable soil restricts many of these wasps to areas of loess or alluvium and thus pushes many species into close proximity. In these restricted areas, the build-up of non-specific parasites may play a major role in permitting such a diversity of species to co-exist (see, e.g., Paine, 1966).

I have attempted to delineate a few of the food relationships in the areas of study in Text-figure 2. Obviously, the arthropods used as prey by the wasps have other natural enemies, some of them in themselves serving as prey for wasps. The common orb-weaving spider *Araneus patagiatus,* for example, is the major prey of *Episyron quinquenotatus,* but itself preys on the small flies that provide the major prey of *Oxybelus* and *Crossocerus.* Thus an increase in the population of *Episyron* might permit an increase in the species of the latter two genera. The Ichneumonidae preyed upon by *Philanthus zebratus* are parasites of caterpillars, some of which may serve as prey of *Ammophila* and other wasps. Thus a high population of *Philanthus* might favor such a wasp as *Ammophila azteca*—except that, ironically, *P. zebratus* also preys directly upon *Ammophila. P. pulcher* preys upon cuckoo wasps to some extent, including species known to attack other ground-nesting wasps. The species of *Philanthus,* indeed, provide the most interesting elements in this fauna, preying as they do on so many wasps, wasp parasites, and parasites of other insects—also, of course, on many bees, which to a certain extent compete with wasps for nesting sites and nectar sources.

Insufficient information is available to explore these interrelationships further—in fact, I have already gone farther than the data warrant—and I should like to turn to the second question posed at the beginning of this section: to what extent

are species differences in behavior understandable in the contexts of interspecific competition and of widespread parasitization?

BEHAVIOR PATTERNS AS ADAPTATIONS TO LIFE IN THE COMMUNITY

There exists a very extensive literature describing the behavior patterns of solitary wasps, for it is true that these patterns are subject to relatively little intraspecific variation and that species differences, even between closely related forms, are often pronounced. However, few attempts have been made to explain these different behavior patterns in terms of their adaptive value. Why do related species often show pronounced differences in prey preferences, manner of approach to the nest, nest closure, mound-leveling, accessory burrows, and so forth? In my opinion the two factors emphasized here—competition and parasitism—are sufficient to explain the adaptive value of nearly all of the species-specific behavior patterns of solitary wasps (see also Evans, 1966a, Chapter XV).

Behavior Related to Competition[1]

The relatively high degree of ecological displacement among the wasps of Jackson Hole is by no means a unique phenomenon; a very similar picture is presented by the solitary wasps of eastern Massachusetts, for example. Indeed, that ecological homologues cannot coexist is a widely recognized biological phenomenon (DeBach, 1966). There are no well-documented exceptions among the wasps of Jackson Hole, for those few species appearing to have identical or broadly overlapping food niches occupy different nesting sites—and this in itself suggests that they may hunt in somewhat different areas. Obviously several sets of behavior patterns are involved here: selection of a nesting site; construction of a nest compatible with that soil type; selection of a hunting site; and response to a particular kind of prey.

No studies were made of hunting behavior, but it can be assumed that even slight differences in prey selection involve important differences in responses to stimuli. A given species of wasp may be narrowly or fairly broadly adapted with respect to prey selection. *Aphilanthops subfrigidus*, which (like its congeners) preys only on queen ants of the genus *Formica* during their nuptial flights, must have highly specialized hunting behavior indeed. On the other hand, *Bembix americana spinolae* is known to forage widely and to respond to Diptera of various shapes and sizes—including such diverse flies as asilids, tabanids, and sciomyzids. *Aphilanthops* has the advantage of being the only wasp in this area using *Formica* ants as prey, but the success of these wasps is very much tied up with the size of nuptial flights and weather during such flights. *Bembix* uses large numbers of deerflies (*Chrysops*) when these are plentiful (a prey not known to be used by other wasps in this area), but when they are not in abundance it is readily able to utilize small muscoids (a common prey of *Oxybelus*) or beeflies (the almost exclusive prey of *Steniolia*). Such a broadened response to potential prey may have evolved in an area where there were fewer species of digger wasps and no competitors for larger flies. Under conditions of severe competition, one would expect a narrowing of the spectrum of response, perhaps at first non-genetic but later becoming fixed in a local population. Under conditions of prolonged

[1] It may be argued that neither food or nesting sites have been shown to be in short supply, and thus competition cannot be demonstrated. But, as pointed out in this section, speed is important to these short-lived insects, and if two species prey on the same thing or nest in the same place, any interference or diminution in space or in the numbers of prey which lengthens their nesting cycles will result in a reduction in number of offspring. I use the word "competition" in this broad sense, to include any interspecies rivalry that is selectively disadvantageous (see also DeBach, 1966).

isolation, such a population might emerge as a species with restricted prey preferences.

There is evidence that various species of *Bembix* show differences in prey type in various parts of their ranges, though to what extent this is genetically determined is unknown. The same is true in *Philanthus*. *P. pacificus*, for example, has been studied at Antioch, California, and found to prey upon wasps and bees in approximately equal numbers, also on parasitic Hymenoptera such as Braconidae and Ichneumonidae (Powell and Chemsak, 1959). *P. crabroniformis* has been observed at Delta, Utah, capturing honeybees at the hive entrances (under the name *flavifrons* Cresson; G. E. Bohart, 1954). Both of these species prey very largely on small halictid bees in Jackson Hole.

It should be pointed out that the success of a predatory wasp is very much dependent upon the speed with which it is able to find and capture prey; if it is forced to search for an uncommon prey or to subdue an unusual prey, the result will be that during its limited lifetime each female will have time to provision fewer cells than usual. This being true, there will be great selective advantage in finding and capturing a particular kind of prey quickly, that is, toward more specialized hunting behavior. My observations on *Steniolia obliqua* hunting beeflies (Evans and Gillaspy, 1964) suggest that it is a much more effective predator on these swiftflying Diptera than is *Bembix*. Thus *Bembix* may be at a disadvantage if forced to rely heavily on beeflies in an area where a specialist on beeflies, *Steniolia*, is abundant.

As already pointed out, related wasps seldom nest in identical sites. This results in a partitioning of available space and also tends to disperse aggregations of different species such that their hunting arenas are at least partially separate. Occupation of different soil types also influences the type of nest. Species nesting in highly friable, dry sand tend to make a series of separate nests, often with one or a few cells; presumably such nests are less amenable to wholesale destruction by parasites than nests in which many cells arise from a single burrow. But in hard-packed, stony soil this presumed advantage is outweighed by the problems of digging. That is, it is advantageous for a species such as *Philanthus crabroniformis* to make a single burrow and ultimately to prepare many cells from it, even though such a nest may be more subject to parasitization by cuckoo wasps or *Phrosinella* flies than a more temporary nest with only a few cells. The female *Philanthus crabroniformis* requires several days to dig her burrow, while *P. pacificus* may complete a burrow in a sand bar in a few hours. The first species usually nests from a single burrow throughout its life, making fifteen or more cells (Fig. 38), while the second prepares a series of shallow nests, each with about three cells (Fig. 35). The correlation between soil texture and number of cells per nest is by no means absolute, but it is true that most of the nesters at MOR-B made multicellular nests (e.g., *Astata nubecula*, two species of *Eucerceris*, and *Belomicrus forbesii*) although a few prepared cells from pre-existing burrows (*Cryptocheilus terminatum*, and *Pisonopsis clypeata*). Here again, speed of work is important to a wasp living only a few weeks, and those species nesting in relatively intractable soil have evolved mechanisms for reducing the total amount of digging that must be done.

Behavior Related to Parasitism

I include here all behavior that appears to function in reducing the success of natural enemies. It is, of course, possible to consider these behavioral devices also as a form of competition. Crombie (1947) remarks that "agencies such as predators may produce a different kind of competition rather than preventing it altogether. They may, for instance, prevent compe-

tition for food among their hosts, but cause them to compete to avoid the predators, e.g., there may be selection for reflexes which assist this." I would agree with this statement, but nevertheless feel that it is useful to distinguish between direct interspecies competition and the competitive success of various species in reducing the attacks of natural enemies.

For example, prey selection is evidently related to interspecies competition, since it results in a partitioning of the available resources, as already pointed out. However, the manner in which the prey is carried to the nest has apparently evolved in response to parasite pressure, as I have argued elsewhere (Evans, 1963a). Jackson Hole has many wasps that carry the prey with their mandibles, but these wasps must either deposit the prey while they open the nest, thus rendering the prey temporarily unprotected against satellite flies, tiger beetles, ants, and so forth; or they may simply leave the nest open, making it available to beeflies, hole-searching miltogrammine flies, and so forth. Jackson Hole also has many species that carry the prey with their middle legs, where it is well protected beneath the body and where it remains while the nest entrance is opened with the front legs. Only one species in this area carries the prey on the end of its abdomen, but that is one of the commonest species, *Oxybelus uniglumis quadrinotatus*. This species is a very rapid provisioner, and I assume speed has been selected for at the expense of exposing the prey to satellite flies.

Two of the larger species of *Philanthus*, both heavily attacked by *Senotainia* flies, exhibit strikingly devious flight patterns upon approaching their nest with prey. In the case of *P. crabroniformis*, prey-laden females (whether or not followed by satellite flies) almost always fly not directly to the nest but to a low herb or grass blade 0.5–2.0 m from the entrance. Here they often cling for a few seconds before proceeding to another perch or (if no flies are present) to the nest. Once at the entrance, females almost always dig through the closure and enter, even though a satellite fly may have appeared in the meantime. Some females followed by flies move about from perch to perch (always within 20 cm of the ground) at varying distances from the nest for as long as five minutes before entering. On several occasions females were seen to lose their would-be parasites before reaching the nest.

The corresponding flight patterns in *P. zebratus* differ in some details. These wasps, with their generally rather large prey, typically descend into the nesting area from a considerable height, landing with an audible sound on the ground and sitting motionless for several seconds before continuing to the nest. If followed by satellite flies, they fly off close to the ground in a circuitous pattern, often disappearing from sight for several seconds to a minute or two. This may be repeated several times if the flies persist or reappear. Although prey-laden females may land on the ground occasionally, they seldom land on vegetation in the manner of *crabroniformis*. Some females followed by flies rise high in the air and descend abruptly as in their initial return flight.

These two species of *Philanthus* are also the only wasps in Jackson Hole known to maintain accessory burrows. These short burrows are dug beside the true burrow and are left open while the true burrow is closed. In *crabroniformis*, a nester in hard soil, newly completed nests lack an accessory burrow, but as females replace their closures again and again they often scrape much of the soil from small quarries beside the nest entrance, so that within a few days numerous nests have such quarries, later in the season still more. For example, on August 3, I counted 26 nests, of which four had one quarry each. On August 12, a count of 40 nests (including all of the original 26) showed that about half had quarries, several of them two (one on each side or both on one side). The quar-

ries varied in depth from 2 mm to 2.5 cm. Females were often seen entering the quarries and occasionally remaining within them for a few seconds. Their primary function was unquestionably as a source of fill in this hard soil. I did not observe any parasites being attracted to them, although it is probable that this sometimes occurs (for a general discussion of accessory burrows, see Evans, 1966b).

P. zebratus nests in much more friable soil, yet some females appear to quarry much of the sand for closure at one or two points, creating short accessory burrows which may be redug from time to time. On August 2, I estimated that 20 per cent of the nests had accessory burrows, and there was no evidence of an increase as the season progressed. Actually, about half of these nests had two such burrows, and several had three. They varied from barely measurable to 3 cm in depth. On three occasions hole-searching flies, *Metopia argyrocephala*, were seen entering these accessory burrows. It seems probable that in *zebratus* the burrows serve a more important role in diverting parasites, than as a source of soil.

These two species of *Philanthus* do not level the mound of soil at the nest entrance, merely leaving it in a fan-shaped pile. In contrast, mound-leveling behavior following completion of a new nest is elaborate in *P. pulcher* and *pacificus*. Mound-leveling behavior is also elaborate in *Bembix americana spinolae*, although absent in the related wasps *B. amoena* and *Steniolia obliqua*. In *Ammophila azteca* and other species of this genus quite another method of removing soil from the edge of the burrow is employed: the female carries small loads forward in flight and drops them some distance away. A variation on this "soil-carrying" theme is employed by *Belomicrus forbesi*, the females of which fly swiftly backward from the nest, each time carrying a lump of earth and dropping it on the ground.

It is assumed that removal of the soil from the nest entrance renders the site less evident to parasites (as it does to humans). Cuckoo wasps and *Phrosinella* flies are often seen flying from one nest entrance to another, landing on the mound of soil and searching about for covered holes. They will also alight, as least briefly, on artificial piles of sand placed in nesting areas, suggesting that their initial attraction is to the sight of the mounds.

Closure of the nest entrance between hunting flights is also regarded as a device for rendering the nest less visible and also for delaying or preventing the entry of diggers such as *Phrosinella* or *Parnopes*. This belief is supported by observations and simple experiments. Bombyliid flies oviposit into many kinds of holes, including artificial holes made by a pencil in the soil. *Metopia* flies also enter various open holes, including blind accessory burrows, as mentioned above. There is, however, a paradox here: *Phrosinella* evidently is not attracted to open holes, but only to closed nests (though presumably preferring thin closures to thick ones); and *Senotainia* is favored by closures, since they cause the wasps to pause at the entrance to dig it open and thus provide a better target for larviposition. The fact that the vast majority of the fossorial wasps of Jackson Hole do maintain a closure suggests that these factors are generally outweighed by others, that is, when and where closing behavior evolved *Senotainia* was a less important parasite than some others. The apparent success of *Phrosinella pilosifrons* against *Philanthus* may reflect the fact that although these wasps do close the nest, the closure is usually rather weak.

The species of *Tachysphex* ought to provide unusually good material for a study of the influence of closure on success of parasites, especially since the nests are shallow and easy to excavate. One would assume that the species making no closure (*tarsatus* and *nigrior*) might be more heavily parasitized by *Metopia* and less heavily parasitized by *Senotainia* than the

species that make a closure (*terminatus* and sp. nr. *linsleyi*). On the other hand, the fact that the first two species use relatively larger grasshoppers, which protrude further behind their bodies in transit, may mean that they present a better target for satellite flies, thus offsetting the advantage of quick entry into the nest. Unfortunately, none of the species of *Tachysphex* are abundant in Jackson Hole.

The digger wasps that omit the outer closure include several that make vertical burrows. Such burrows cannot be closed in the usual manner of simply scraping soil into the entrance; either they must be left open, or special mechanisms evolved. The species of *Eucerceris* leave the entrance open, but possibly compensate for this by keeping a certain amount of loose sand in the lower part of the burrow. *Stenodynerus papagorum* makes a vertical burrow, but in this case it is capped by a mud turret (Fig. 23). These turrets may have evolved as deterrents to parasites, but I have seen cuckoo wasps entering them, and Olberg (1959) has provided a photograph of a cuckoo wasp entering the turret of a different species. Although the species of *Ammophila* make short, vertical burrows, they have evolved unique behavior enabling them to close their burrows effectively. Briefly, the female finds an object that just fits the lumen of the burrow, fits it in place, then puts additional lumps and loose soil above it (Fig. 31).

Final closure of the nest in *Ammophila azteca* is also enhanced by the "tool using" behavior of this species, which surely serves to provide a firm barrier against parasites and to form a plug which does not erode and expose the location of the shallow nest to predators. Many other wasps make a fairly lengthy final closure (*Bembix americana spinolae* and *Philanthus pulcher*, for example), but whether the species of *Philanthus* that nest in one burrow for their entire lives usually fill up the burrow before they die is doubtful.

Progressive feeding of the larva probably also arose in response to parasite pressure (Evans, 1966a). In Jackson Hole, *Ammophila azteca*, *Bembix americana spinolae*, and *Steniolia obliqua* are the only known progressive provisioners. Since these wasps require five days or more to complete a single cell (as compared to usually about one day for mass provisioners), they would seem to be at a disadvantage when the seasons are as short as they are here. The three may thrive simply because almost none of the larvae succumb to parasites; as noted above, miltogrammine fly maggots and wasp larvae may both survive in such nests, at least at times. *Ammophila azteca*, furthermore, has evolved an unusual behavioral feature peculiarly adaptive for these short summers: successive nests overlap, the female maintaining two to four nests at different stages of development and remembering the location of each (Evans, 1965).

Admittedly the success of these various behavioral devices has yet to be documented quantitatively. In fact, it is uncertain whether it can be, both because of the difficulty in obtaining such data for ground-nesting species and because the data, if obtained, may not mean a great deal. The parasites and their hosts have undoubtedly undergone a measure of coevolution, and if a particular behavioral device does not seem effective, it may mean that the parasites are, at this stage, "one step ahead."

Summary of Behavioral Adaptations

No two of the wasp species studied in Jackson Hole are behaviorally alike in every respect. This suggests that each has evolved to meet somewhat different problems. There is no way of knowing where or when these distinctive patterns evolved. The present is the only time-transect we have, and the interplay among the various members of the fauna today can only suggest some of the problems these species have surmounted. At least in this context many otherwise puzzling behavior patterns

"make sense." Our explanations may not be complete, or even correct, but at least they provide the basis for a fuller understanding of the biological role of each species attribute than any amount of study of museum specimens is likely to provide.

In these restricted areas of bare, friable soil in Jackson Hole—and in similar areas elsewhere—a wasp must have certain behavioral capabilities in order to be successful. Some of these are as follows:

(1) It must hunt prey which is readily available and not overly exploited by other predators, and its hunting behavior must be closely attuned to the habitat and behavior of that particular prey.

(2) It must utilize available sources of nectar or honeydew for its own nourishment without undue interference or overexploitation of the source by bees or other wasps.

(3) It must nest where there is available space not densely filled with other wasps or with ground-nesting bees, and it must construct a nest appropriate to that soil type.

(4) It must be able to provision its nest quickly and with a minimum of delay due to prey scarcity or to interference from other wasps or from parasites, especially in an area with a short summer season.

(5) It must possess mechanisms for reducing the success of parasites to such an extent that each female is able to leave at least two progeny that survive to adulthood. Examples of such mechanisms include pedal prey carriage, devious flight patterns, nest closure, mound leveling, accessory burrows, progressive provisioning, and so forth.

Possession of these attributes in various forms—and, of course, such other obvious ones as the ability to survive the winters at this latitude and altitude—has enabled these species to coexist, some with greater success than others. Paradoxically, it may be the presence of so many natural enemies that permits so many species to occur together, as discussed earlier; yet each species appears committed to evolutionary strategies for incurring a lessened incidence of successful attack by these enemies.

It may be instructive to summarize these strategies for the species of one genus. *Philanthus* has five species in Jackson Hole, and, by coincidence, five common species in eastern Massachusetts (all different). Eventually I hope to complete a detailed comparative study of these ten species, but for the present I offer a tabular comparison of some of the more salient attributes of each (Table 1). In each area there are certain species in which mound-leveling is well developed (all of these are members of the *politus* species-group). In each area there are species in which accessory burrows are sometimes constructed, and in the eastern states one (*lepidus*) in which such burrows form a fixed feature of behavior (although varying in number). All Jackson Hole species make a nest closure, but two eastern species omit the closure. Such differences presumably reflect the relative importance of satellite flies, beeflies, and other natural enemies at the times and places when these behavior patterns evolved; e.g., open nest entrances permit rapid entry and may reduce the success of *Senotainia*, while permitting access to the nest by *Metopia*, beeflies, etc. Others (prey type and soil type, also size, time of emergence, and other qualities not tabulated here) probably represent mechanisms for reducing direct competition with congeners. A similar analysis of other genera would provide a very similar picture.

It is obvious that the functional significance of these various behavior patterns remains unproved. The conclusions I have drawn are based on extensive field work in Jackson Hole and elsewhere, but I would be the first to admit the need for many more observational data, for experiments designed to test critical points, and for mathematical approaches such as those of many contemporary population biologists.

TABLE I

COMPARISON OF TEN SPECIES OF *Philanthus* WITH RESPECT TO SIX BEHAVIORAL FEATURES.

Species	Nest type[1]	Soil type[2]	Prey type[3]	Levels mound at entrance	Temporary closure	Accessory burrows
			Jackson Hole, Wyoming			
pacificus	S	1	SB	+	+	0
pulcher	S	2	BW	+	+	0
crabroniformis	P	3	SB	—	+	0–2
zebratus	P	2	BW	—	+	0–3
bicinctus	P	3	LB	—	+	0
			Eastern Massachusetts			
politus	S	1	SB	+	+	0
gibbosus	P	2	SB	—	+	0–2
lepidus	S	1	SB	—	+	1–5
solivagus	P	1a	BW	—	—	0
sanbornii	P	2	LB	—	—	0

[1] Nest type: S—a succession of simple nests with few cells.
P—a more or less permanent, multicelled nest.
[2] Soil type: 1—light, fine-grained sand; 1a—such sand, but only on slopes.
2—coarse, moderately friable sand.
3—very coarse-textured sandy gravel.
[3] Prey type: SB—small bees; LB—large bees; BW—both bees and wasps used in numbers.

The complexity of these communities is such that they must be examined from many points of view. A behavioral adjustment on the part of one species, or the extinction of a species or arrival of a new one—or, indeed, the varying population sizes of each species belonging to the community, even peripherally—each of these factors may have subtle effects upon many members of the community. Hence no factor, no behavior can a priori be regarded as unworthy of study. The twin sciences of ecology and ethology are certain to become increasingly important with our growing concern with the environment and our growing awareness of its complexity. Despite welcome advances in theory and the promise of computerization, it appears that the need is greater than ever for what is sometimes called "old fashioned natural history."

ANNOTATED LIST OF WASPS OF JACKSON HOLE

The following is a list of wasps collected in the areas of study, with a brief summary of their nesting behavior, if known. Arrangement of families and genera is the conventional one, approximating that in the Second Supplement of the Synoptic Catalog of North American Hymenoptera (Krombein and Burks, 1967). A few species taken outside the immediate area of study are included but are enclosed in brackets. The major localities were described earlier (see "Study Areas"), but the abbreviations used are repeated here for the sake of ready reference:

ELK: 4 miles SW of the Elk Post Office (Map 1);

HHS: Huckleberry Hot Springs, Teton National Forest;

JAC: 5 miles north of Jackson;

MOR: Moran, near Jackson Hole Research Station (Map 1);
MOR-A: Largely restricted to alluvial sand;
MOR-B: Chiefly in bare places in lower outwash plain;

PCR: Pilgrim Creek, 4 to 7 miles NE of Moran.

Records of adults feeding on the nectar of flowers are also included, and again several abbreviations have been employed:

Eri: *Eriogonum* spp. (wild buckwheat);

Per: *Perideridia gairdneri* (yampa);

Sol: *Solidago* spp. (goldenrod);

Several species were taken in Malaise traps set up in MOR-A1, but not elsewhere. These are identified simply by the word "trap."

The insect fauna of Jackson Hole is by no means thoroughly known, and in a number of cases I have been able to identify wasps only to genus. Some species identifications may prove incorrect as the systematics of Hymenoptera improves. However, all material collected has been placed in the collections of the Museum of Comparative Zoology, and specimens with associated behavioral data are cross-referenced by number to my field notes, also on permanent file at the Museum. Thus, if problems arise regarding the identity of any of the species studied, it should be possible for specialists to re-examine this material.

I identified many of the wasps myself, but received valuable help from several persons, especially from R. M. Bohart (Chrysididae, Eumenidae, and certain Sphecidae), A. S. Menke (*Ammophila*), F. D. Parker (Astatinae and *Leptochilus*), F. E. Kurczewski (*Tachysphex*), and K. V. Krombein (various Sphecidae). Most of the prey were identified by various specialists located at the U. S. National Museum, but H. W. Levi identified the spiders, and H. J. Reinhard and F. C. Thompson assisted with the flies. P. H. Timberlake undertook the arduous task of identifying the many bees taken as prey by species of *Philanthus*.

Family DRYINIDAE

These small wasps are parasites of leafhoppers and plant hoppers; they make no nest but leave the prey on vegetation, where it recovers from paralysis and continues feeding. The American species have been little studied, and species identification is nearly impossible.

Chalcogonatopus sp. MOR, July 28–Aug. 15, 1 ♀, 2 ♂♂.

Anteon sp. MOR, July, 1 ♂ in trap.

Aphelopus comesi Fenton. MOR, Aug., 1 ♂ in trap.

Family CLEPTIDAE

Cleptids have been reared from sawfly larvae. Only one species has been taken in Jackson Hole.

Cleptes provancheri Aaron. MOR, July 11–Aug. 16, 5 ♀♀, 1 ♂, ♀ on Per, one ♀ in trap; PCR, Aug. 2, 1 ♀, 1 ♂.

Family CHRYSIDIDAE (Cuckoo wasps)

Cuckoo wasps are parasites of various wasps and bees, usually entering the nest and laying their egg while the host is absent. A good recent account of several species is provided by Krombein (1967). Although cuckoo wasps are abundant in Jackson Hole both in individuals and in numbers of species (24), I obtained no important new information regarding their biology.

Omalus aeneus (Fabricius). MOR-B, July 6–30, 1 ♀, 2 ♂♂; note no. 1981: 1 ♀ taken from a nest of *Philanthus pulcher*, as prey. This wasp is known to parasitize species of *Passaloecus*, *Pemphredon*, and *Stigmus* nesting in cavities in wood.

Omalus plicatus (Aaron). MOR-B, Aug. 1, 1 ♀.

Omalus purpuratus (Provancher). MOR-A, July, 2 ♀♀, in trap.

Omalus speculum (Say). MOR, July 28–Aug. 1, 1 ♀, 1 ♂.

Omalus variatus (Aaron). MOR, July 19–Aug. 13, 1 ♀, 2 ♂♂; ELK, July 10, 1 ♀.

Elampus viridicyaneus Norton. MOR, July 11–Aug. 3, 5 ♀♀; JAC, July 15, 2 ♀♀. Note no. 2110B; 1 ♂, MOR-B3, taken from nest of *Philanthus pulcher* as prey.

Holopyga hora Aaron. MOR, July 16–30, 2 ♀♀.

Holopyga ventralis (Say). MOR-B, July 11–Aug. 11, 2 ♀♀, 4 ♂♂, ♀♂ on Sol, Per; ELK, Aug. 4. 1 ♂; PCR, Aug. 2, 1 ♀. Note no. 1981: 1 ♀, MOR-B3, taken from nest of *Philanthus pulcher*, as prey.

Hedychridium fletcheri Bodenstein. MOR, July 11–Aug. 23, 8 ♀♀, 4 ♂♂; ELK, Aug. 4, 1 ♂; HHS, July 17, 1 ♂. Note nos. 1981, 1984, 2118: 1 ♀, 3 ♂♂, MOR-B3, taken from nests of *Philanthus pulcher*, as prey. Note nos. 2096, 2109: 2 ♀♀, both taken on ground in *P. pulcher* nesting areas, MOR-B3, July 14, 21, 1967.

These females were flying from one nest entrance to another, apparently attracted by the fresh earth at the entrances. They were not seen to enter any nests (other wasps and various bees were also nesting here). The species of this genus apparently attack ground-nesting wasps; *H. fletcheri* is reported to attack *Tachysphex*, while some European species are said to attack *Dienoplus* spp.

Hedychrum nigropilosum Mocsary. MOR, Aug. 1, 1 ♂.

Hedychrum parvum Aaron. MOR, July 16–Aug. 14, 1 ♀, 3 ♂♂, ♂ on Per. Note no. 2048: ♀ found in burrow of *Eucerceris fulvipes* Cresson while I was digging out nest, Aug. 14, 1964, MOR-B1. Since other species of this genus are known to attack *Cerceris* spp., it seems probable that this individual was in fact attacking *E. fulvipes*.

Chrysura densa (Cresson). MOR, July 6, 1 ♂; Death Canyon, Aug. 15, 1 ♀.

Chrysura pacifica (Say). JAC, July 15, 1 ♀; MOR, July 4–16, 3 ♀♀, 2 ♂♂, 1 ♂ no. 1981: taken as prey by *Philanthus pulcher*.

Ceratochrysis cyanosoma (Mocsary). MOR, Aug. 26, 1 ♀.

Ceratochrysis perpulchra (Cresson). MOR, July 13, 1 ♀; PCR, Aug. 2, 1 ♀.

Ceratochrysis trachypleura Bohart. MOR, July 20–Aug. 26, 11 ♀♀, 3 ♂♂; ELK, July 28, 1 ♀; HHS, Aug. 11, 1 ♀. Note nos. 1996, 2109, 2135, all MOR-B, July, Aug.

Several females were seen landing at nest entrances and walking over soil at entrances, but not entering; nests were those of *Philanthus pulcher*, *P. crabroniformis*, and *Ammophila azteca* (cuckoo wasp erroneously identified as *Ceratochrysis perpulchra* in my 1965 paper on *A. azteca*). This species is common in Jackson Hole and is surely a parasite of one or more species of ground-nesting wasps or bees, but I have no evidence as to which ones. *C. perpulchra* is reported as a parasite of *Ammophila aberti*, but the type species of the genus, *enhuycki* Cooper, is a parasite of the twig-nesting eumenid *Leptochilus*. There are two distinct color forms of female *trachypleura* in Jackson Hole, one blue-green, the other with a strong overlay of coppery and rose tints; the two are represented in about equal numbers.

Trichrysis doriae (Gribodo). MOR, July, Aug., 3 ♀♀, in trap.

Chrysis coerulans Fabricius. MOR, July 11–Aug. 15, 9 ♀♀, 1 ♂, several in trap; ELK, Aug. 4, 1 ♂; PCR, Aug. 2, 1 ♀. This species attacks various twig-nesting Vespidae; Krombein (1967) has recently discussed its biology.

Chrysis derivata Buysson. MOR-A, July, 1 ♀, in trap. Also known to be a parasite of twig-nesting Vespidae.

Chrysis dorsalis Aaron. MOR-B, Aug. 1–26, 3 ♀♀, 1 ♂, ♀♂ on Per.

Chrysis pattoni Aaron. MOR, July 7, 1 ♂; HHS, July 17, 1 ♀.

Chrysis snowi Viereck. MOR, July 16, 1 ♂.

[**Chrysis stenodyneri** Krombein. South Gate, Yellowstone National Park, July

19, 1 ♀. This species and *pattoni* are both reported to attack twig-nesting Vespidae.]

Chrysis venusta Cresson. MOR-A, July 16–Aug. 3, 2 ♀♀. Note no. 2108: 1 ♀, seen entering the mud turret at a nest of *Stenodynerus papagorum* and coming out again within a few seconds. It is possible that this species attacks ground-nesting rather than twig-nesting Vespidae.

Parnopes edwardsii (Cresson). MOR-A, July 18–Aug. 26, 17 ♀♀, 2 ♂♂; ELK, Aug. 4, 1 ♀; HHS, July 17, 1 ♀. Note nos. 1819, 1987, 1997, MOR: females commonly seen in the nesting sites of *Steniolia obliqua* and *Bembix americana spinolae* (and observed digging into nests of the former species). This is a known parasite of *S. obliqua* and *B. americana comata*, and is a probable parasite of other Bembicini (for details see Evans, 1966a).

Family SIEROLOMORPHIDAE

Nothing is known of the biology of these wasps. One species is common in Jackson Hole, and is usually collected by sweeping low vegetation in sandy places.

Sierolomorpha nigrescens Evans. MOR, July 12–22, 1 ♀, 16 ♂♂.

Family TIPHIIDAE

Only four species of this large family have been taken in Jackson Hole, all on sandy soil near the Snake River.

Tiphia sp. near **essigi** Allen. MOR, July 29–Aug. 11, 4 ♀♀, 3 ♂♂, ♀♂ on Per; ELK, Aug. 4–10, 5 ♂♂. Species of this genus are parasites of white grubs (Scarabeidae).

Tiphia infossata Allen. MOR, July 12, 1 ♀.

Methocha stygia (Say). MOR-A, July 16, 1 ♀. Species of this genus attack the larvae of tiger beetles in their burrows in the soil. The single female taken in Jackson Hole has a dull, striate thoracic dorsum like other females from the northwestern states and western Canada. It is possible that these will prove specifically or subspecifically distinct from *stygia*.

Myrmosa unicolor Say. MOR, July 11–24, 1 ♀, 3 ♂♂, 2 ♂♂ in trap. This wasp has been reared from cocoons of *Tiphia*.

Family MUTILLIDAE (Velvet ants)

The two species of mutillids occurring in Jackson Hole are both relatively uncommon; both may be parasitic on ground-nesting bees.

Dasymutilla myrice Mickel. JAC, July 25, 2 ♂♂.

Dasymutilla fulvohirta (Cresson). MOR, Aug. 17–26, 2 ♂♂; JAC, July 25, 1 ♂.

Family SAPYGIDAE

Sapygid wasps are parasites of bees. I have taken only two specimens in Jackson Hole.

Eusapyga rubripes proxima (Cresson). MOR, July 16, 1 ♂.

Sapyga confluenta Cresson. MOR, July 30, 1 ♀.

Family EUMENIDAE (Mason wasps)

These wasps carry water to moisten dry soil, the resulting pellets being used to make free mud nests, to partition off cells, or to build mud turrets. All species use eruciform larvae as prey and oviposit in the empty cell before prey is brought in. In Jackson Hole, I have collected 24 species, but only one of these, *Stenodynerus papagorum*, nests in numbers in the soil in the study areas.

Eumenes crucifera nearcticus Bequaert. MOR, July 29–Aug. 26, 2 ♀♀, 5 ♂♂, ♀♂ on Sol. This species, like the follow-

ing two, makes mud pots attached to twigs and provisions with caterpillars. I found no *Eumenes* nests in Jackson Hole.

Eumenes iturbide pedalis Fox. MOR, July 20, Aug. 12, 1 ♀, 1 ♂.

Eumenes verticalis coloradensis Cresson. MOR, July 8–Aug. 14, 3 ♀♀, 7 ♂♂; PCR, Aug. 2, 1 ♂; JAC, July 25, 1 ♀; Death Canyon, Aug. 15, 1 ♀.

Odynerus dilectus Saussure. JAC, July 15–25, 1 ♀, 1 ♂. This species is known to be a ground-nester and to surmount its burrow with an erect turret up to 2 cm high (Linsley and Michener, 1942).

Pseudepipona herrichii aldrichi (Fox). MOR, July 14–Aug. 23, 4 ♀♀, 2 ♂♂, ♀ on Sol.

Euodynerus auranus (Cameron). MOR, July 29–Aug. 3, 1 ♀, 1 ♂, ♂ on Sol.

Euodynerus castigatus (Saussure). MOR, Aug. 17–26, 1 ♀, 2 ♂♂, ♀ on Per, ♂ on Sol; ELK, Aug. 4, 1 ♂, note no. 2032: taken as prey of *Philanthus zebratus nitens*. Evidently the nest of this species has not been described. I have taken the liberty of including a photograph of a five-celled mud nest found under a stone in a field near Ithaca, N. Y. (note no. 1144; Fig. 22); several adults were reared from this nest.

Euodynerus f. foraminatus (Saussure). Death Canyon, Aug. 15, 1 ♂. Nests in hollow twigs (see especially Krombein, 1967).

Euodynerus leucomelas (Saussure). MOR-B, July 8–Aug. 26, 2 ♀♀, 1 ♂, ♀ on Sol; HHS, Aug. 11, 1 ♂. Also a twig-nester.

Euodynerus tempiferus eldoradensis (Rohwer). JAC, July 15, 1 ♀.

Ancistrocerus adiabatus (Saussure). MOR, July 20–Aug. 10, 3 ♀♀, 2 ♂♂, ♂ on Sol; HHS, July 17–30, 5 ♂♂; PCR, Aug. 2, 2 ♂♂; ELK, Aug. 4–21, 2 ♀♀, 1 ♂, note nos. 2132, 2133 (1 ♀, 1 ♂): taken as prey of *Philanthus zebratus nitens*. All but two females are of the white-banded color form called *albolacteus* by Bequaert.

Ancistrocerus a. antilope (Panzer). MOR-B, July 18–Aug. 26, 4 ♂♂, on Sol, Eri; PCR, Aug. 13, 1 ♂. This widely distributed twig-nester has been studied by Cooper (1953), Krombein (1967), and others.

Ancistrocerus c. catskill (Saussure). MOR-B, July 5–Aug. 26, 7 ♀♀, 10 ♂♂, ♀♂ on Sol, Eri; HHS, July 17–30, 1 ♀, 3 ♂♂; PCR, Aug. 2–13, 1 ♀, 1 ♂; JAC, July 15, 1 ♀. Note no. 2019: MOR-B3, July 31, ♂ taken as prey of *Philanthus pulcher*. All but 2 ♀♀ and 5 ♂♂ are of the white-banded color form called *albophaleratus* Saussure; Krombein (1967) has shown that both forms can often be reared from the same trap-nest.

Symmorphus canadensis (Saussure). MOR-B, July 19–21, 2 ♀♀, one of them note no. 2109: taken as prey of *Philanthus pulcher*.

Symmorphus c. cristatus (Saussure). ELK, July 10, 1 ♂. This is a twig-nester, like the preceding species (Krombein, 1967).

Symmorphus meridionalis Viereck. MOR, July 8–Aug. 4, 3 ♀♀; PCR, Aug. 2, 1 ♂; JAC, July 15, 1 ♀; ELK, July 18, 1 ♀, note no. 2126: taken as prey of *Philanthus zebratus nitens*.

Leptochilus erubescens (Bohart). MOR, July 7–Aug. 25, 2 ♀♀, one on Sol.

Leptochilus rufinodus (Cresson). MOR, July 24, 1 ♀.

Stenodynerus anormis (Say). MOR, July 19–Aug. 3, 1 ♀, 1 ♂.

Stenodynerus kennicottianus (Saussure). MOR, July 13, 1 ♂.

Stenodynerus lucidus (Rohwer). MOR, July 4–5, 1 ♀, 1 ♂.

Stenodynerus p. papagorum (Viereck). MOR, July 12–Aug. 11, common; PCR, Aug. 13, 1 ♀; HHS, July 17, 1 ♀. Note nos. 1992 and 2098A, MOR-B, ♀ and ♂ taken as prey of *Philanthus pulcher*. Note nos. 2003, 2015, 2039, 2108, MOR-A, July 23–Aug. 11, 1964, 1967: nesting behavior.

This species nested in considerable numbers in one small area of flat, rather hard-packed sand three to five meters from the Snake River; in 1967 there were at least 30 nests here, the entrance sometimes only 2–5 cm apart. In addition, an occasional nest was noted along sandy roads and paths farther from the river. Each nest was surmounted by an entrance tube constructed of small mud pellets, the tube making a right angle to the burrow and running along the surface of the ground, usually for 1–2 cm, but one exceptional entrance tube 4 cm long was found (Fig. 23). These tubes were often destroyed by pedestrians or by heavy rains, and in at least some cases the nests were abandoned after this. The burrows of three nests excavated were vertical, measuring about 5 cm to the most shallow cell, 6–7 cm to the deepest cell. The nests excavated contained from two to five closely clustered, oblique cells, each about 5 × 9 mm in diameter. The cells were separated by mud barriers and each had a rather hard, smooth wall, probably as a result of the soil being softened with water before being removed (Fig. 27).

Females were seen descending from a considerable height with prey, landing on or near the end of the tube, and crawling in with the prey in their mandibles. There was no evidence of a closure anywhere in the tube or burrow. The egg was laid in the empty cell before prey was brought in, and was suspended by a short filament from the top of the cell. The number of prey per cell varied from 14 to 19. All were coleopterous larvae of the families Curculionidae (tribe Anthonomini) or Chrysomelidae (*Xenochalepus* sp.). All appeared to be leafminers, and I assume the wasp removed them from the mines, but this was not observed.

Some of the larvae found in 1964 gave rise to adult wasps in May, 1965, but no parasites were reared. In July, 1967, I noted that females were often followed by satellite flies, *Senotainia trilineata* Wulp. Also, a cuckoo wasp, *Chrysis venusta* Cresson, was seen entering the entrance tube of a nest and coming out a few seconds later.

Stenodynerus taos (Cresson). MOR, Aug. 8, ♀, on Per; ELK, Aug. 4, ♀, note no. 2032: taken as prey of *Philanthus zebratus nitens*.

Pterocheilus morrisoni Cresson. MOR, July 7–Aug. 3, 3 ♀♀; ELK, July 10, 1 ♀. So far as known, species of this genus nest in the ground.

Family MASARIDAE

The two species of Masaridae treated here belong to a group known to provision its cells not with paralyzed arthropods, but with pollen and nectar.

Pseudomasaris edwardsii (Cresson). MOR-B, July 8, 2 ♀♀ on dirt road; PCR, July 17, 1 ♀; ELK, Aug. 2, 1 ♂, note no. 2133: taken as prey of *Philanthus zebratus nitens*. This species is known to make mud cells attached to rocks (Hicks, 1929).

[**Pseudomasaris vespoides** (Cresson). South Gate, Yellowstone National Park, mud nest on rock found Aug. 2, 1961 (Fig. 21); male emerged from this nest more than two years later, July 1963.]

Family VESPIDAE (Social wasps)

These wasps make carton nests and provision them with macerate insects of many kinds. I made no effort to collect these wasps exhaustively or to study their behavior, and I present here a mere list of the few specimens collected.

Vespula acadica (Sladen). MOR-B, Aug. 11, 1 ♀ on Per.

Vespula austriaca (Panzer). PCR, July 17, 2 ♀♀. This species lacks a worker caste and is a social parasite of other members of this genus.

Vespula consobrina (Saussure). MOR-B, July 12, 1 ♀.

Dolichovespula arctica (Rohwer). MOR-B, July 16, 1 ♀. This is also a social parasite, attacking the following species.

Dolichovespula arenaria (Fabricius). MOR, July 16–Aug. 26, 4 ♀♀, 1 ♂; PCR, July 17, 1 ♀; JAC, July 15, 1 ♀.

Dolichovespula maculata (Linnaeus). MOR, July 16–30, 3 ♀♀; PCR, Aug. 2, 1 ♀.

Dolichovespula norvegicoides (Sladen). MOR, Aug. 14, 1 ♂; PCR, July 17, 1 ♀; JAC, July 15, 1 ♀.

Family POMPILIDAE (Spider wasps)

Spider wasps nest solitarily and prey upon spiders of approximately their own size, only one spider being used per nest-cell. Thirty species have been taken in Jackson Hole, and there is reason to regard all but one (*Dipogon sayi*) as ground-nesters, or as parasites of ground-nesting Pompilidae, although several of the species have not been studied in the field.

Cryptocheilus t. terminatum (Say). MOR-B, July 24–Aug. 27, common, ♀♂ on Per; HHS, July 17–30, 1 ♀. Note no. 2170, MOR-B3, Aug. 15–27, 1967: nesting behavior.

On August 15, a female was seen entering a vertical cicada emergence hole in a bare place among grasses and herbs 30 meters from river. She entered quickly, without noteworthy searching behavior, without prey. I dug the nest on August 23 and found seven cells, at depths of from 7 to 11.5 cm, each at the end of a short side burrow (2–7 cm long) from the cicada hole (Fig. 33). Each cell measured about 7×12 mm; the cicada hole was 1 cm in diameter and terminated at a depth of 17 cm. All cells were closed with a firm plug of soil; each had a paralyzed spider, venter-up, or a wasp larva or cocoon. The larvae were more or less coiled around the spider's abdomen, feeding through the side. No relationship of depth with age of cell was noted: a cocoon was found at 10 cm, larvae at 7, 8, 9, and 11.5 cm, the one egg at 10.5 cm (remaining cell contained a moldy spider). All spiders appeared to be the same species of *Lycosa,* both sexes; two which were preserved proved to be juvenile males, possibly *L. pratensis* Emerton. On August 27 the same or another female wasp was seen about a meter away plunging into a hole which proved to be a cave-in over a mammal burrow; nest-cells, if present, were not located.

Priocnemis notha navajo Banks. MOR-B, July 27–Aug. 26, 11 ♀♀, 2 ♂♂, ♀♂ on Per, ♀ on Sol, Eri; ELK, Aug. 4, 1 ♀; PCR, Aug. 2, 1 ♀, 5 ♂♂. Other subspp. of *notha* are reported to nest in the soil and use spiders of the families Lycosidae, Clubionidae, and Salticidae.

Priocnemis notha occidentis Banks. MOR-B, July 29, 2 ♀♀, on Per; PCR, Aug. 2, 2 ♀♀.

In this subspecies, characteristic of the Pacific Northwest, the abdomen of the female is wholly rufous (wholly black in *navajo),* but males are indistinguishable from *navajo.* Jackson Hole appears to represent an area of overlap of the two subspecies. Two of the females listed above have a little black on the tip of the abdomen. The following have considerable black (apical .2–.5) and are considered intergrades: MOR-B, July 29–Aug. 26, 7 females, on Per and Sol; PCR, Aug. 2. I took both subspecies and intergrades together on several occasions. The intergrades resemble *n. notha* in color, but all

males from Jackson Hole are all black and have a subgenital plate like that of *navajo* and *occidentis*.

Dipogon sayi nigrior Townes. HHS, July 17, 1 ♀. This is a twig-nester, reported as preying upon *Xysticus* (Thomisidae). *D. s. sayi* has been studied extensively and found to prey largely upon *Xysticus* and other Thomisidae (see Evans and Yoshimoto, 1962).

Ageniella blaisdelli (Fox). MOR-B, July 28–Aug. 23, 12 ♀♀, 3 ♂♂, ♀♂, on Per, ♀ on Sol; ELK, Aug. 4, 1 ♀, on Per. Prey and nesting behavior unstudied.

Ceropales maculata fraterna Smith. MOR, July 12–Aug. 26, 2 ♀♀, 3 ♂♂, ♀♂ on Sol, Eri; ELK, Aug. 4, 1 ♀; HHS, July 17, 1 ♀, 1 ♂; PCR, Aug. 2, 1 ♂. This wasp is a cleptoparasite of *Pompilus scelestus* (Peckham and Peckham, 1898) and probably of other Pompilidae.

Evagetes bradleyi (Banks). ELK, Aug. 4, 1 ♀. This may be no more than a hairy form of *hyacinthinus*. The one female taken resembles the type of *bradleyi* closely.

Evagetes crassicornis consimilis (Banks). MOR, July 4–Aug. 26, 7 ♀♀, 5 ♂♂, ♀ on Sol; ELK, Aug. 4, 3 ♀♀. The nominate subspecies is known to be a cleptoparasite of species of *Pompilus* and *Episyron* (Richards and Hamm, 1939).

Evagetes hyacinthinus (Cresson). MOR, July 18–Aug. 23, 5 ♀♀; PCR, Aug. 2, 1 ♀; HHS, July 17, 1 ♀; ELK, Aug. 4, 1 ♀. Note no. 2020F; MOR-A, Aug. 23, 1967.

Over the previous several days a number of ♀ *Episyron quinquenotatus* were seen nesting in a small sand bank only two meters from the Snake River. On this date an *Evagetes hyacinthinus* was observed digging in this same bank, apparently searching for closed nests of *Episyron*.

Evagetes padrinus padrinus (Viereck). MOR-A, July 18–Aug. 12, 9 ♀♀, 3 ♂♂; JAC, July 15, 1 ♂.

Evagetes parvus (Cresson). MOR, July 28–Aug. 14, 2 ♀♀, 2 ♂♂, ♂ on Per; ELK, Aug. 4–10, 1 ♀, 4 ♂♂; PCR, Aug. 2, 3 ♂♂; HHS, July 17, 1 ♀. A cleptoparasite of various species of *Anoplius* and *Pompilus* (Evans and Yoshimoto, 1962).

Evagetes subangulatus (Banks). MOR-B, July 12–Aug. 14, 3 ♀♀, 3 ♂♂; ELK, Aug. 4–13, 3 ♀♀, 1 ♂, ♀ on Per; HHS, July 17–30, 5 ♀♀, 2 ♂♂; PCR, 4 ♀♀, 4 ♂♂, Aug. 2–13.

Episyron biguttatus californicus (Banks). MOR-B, July 15–Aug. 26, 4 ♀♀, 2 ♂♂, ♀ on Sol, ♂ on Per; ELK, Aug. 4, 1 ♀; PCR, Aug. 2, 1 ♂. A predator on orb-weaving spiders (Wasbauer and Powell, 1962).

Episyron oregon Evans. MOR-B, July 6–Aug. 26, 4 ♀♀, 1 ♂, ♀ on Sol; PCR, Aug. 13, 1 ♂; HHS, July 17, 1 ♀. Note no. 2000, near Ashton, Idaho, July 21, 1964.

At 1600 hours, a female was seen dragging a male *Araneus trifolium* (Hentz) backward across a sandy road through a clearing in an evergreen forest. She carried it up the stems of grass and weeds several times, flying off with it but gaining little distance because of the weight of the spider. Wasp and spider were taken for identification.

Episyron q. quinquenotatus (Say). MOR-A (also B, nesting in earth piles thrown up by ground squirrels), July 4–Aug. 26, very common, ♀♂ on Sol, Per, Eri; ELK, Aug. 4–10, 2 ♀♀, 1 ♂; PCR, July 17, 1 ♂. Note nos. 2001, 2120, July 23–Aug. 16, 1964, 1967: nesting behavior.

An exceedingly common wasp throughout the summer, restricted to areas of sand or powdery earth; males often swarm over

the sand in the morning hours. I saw many females with prey and took eleven; seven were adult *Araneus patagiatus* Clerck (6 females, 1 male), and four were juvenile *Araneus*. Females commonly place the spider in the crotch of a plant while digging the nest (Figs. 6, 7). After closure, they often pick up twigs and pebbles and place them over the nest site. The nesting behavior of this species has been reported elsewhere (see Evans and Yoshimoto, 1962, and Evans, 1963b; Kurczewski and Kurczewski, 1968, have presented 238 prey records, all Araneidae, a large number of them *Araneus patagiatus*). *Senotainia trilineata* is a known parasite.

Anoplius hispidus (Dreisbach). MOR-B, July 7–15, 6 ♂♂. I have considered *hispidus* a synonym of *cylindricus* Cresson (Evans, 1951), but since the latter may be a complex of several closely related species and since the Jackson Hole specimens are close to the type of *hispidus*, I list them under this name.

Anoplius percitus Evans. PCR, Aug. 2, 1 ♀. This is the westernmost record for this species.

Anoplius tenebrosus (Cresson). MOR, July 4–Aug. 26, common, ♀♂ on Sol, Per; also common throughout summer at ELK, JAC, PCR, HHS.

Females taken in early July often have tattered wings, suggesting that they overwinter as adults; males and freshly emerged females appear about July 20; a mating pair was taken on August 2. This species is known to prey upon Lycosidae and Thomisidae (Evans and Yoshimoto, 1962). Throughout its range the females emerge early in the season. A previously unpublished record from Gull Lake, Michigan, reveals that females take spiders very early in the season in that state (May 12, 1967; immature *Lycosa baltimoriana* Keys.). A second previously unpublished note (no. 1899, Lexington, Massachusetts, June 30, 1963) indicates that this species suspends its prey from the crotch of a plant in the manner of *Episyron quinquenotatus* and other species (prey: *Thanatus formicinus* (Oliv.), female Thomisidae).

Anoplius ithaca (Banks). MOR-A, July 16, 1 ♀. Known to prey upon Lycosidae along watercourses (Evans and Yoshimoto, 1962).

Anoplius imbellis Banks. MOR-A, July 4–Aug. 14, 2 ♀♀, 6 ♂♂; HHS, July 11, 1 ♀. Also known to prey upon Lycosidae along watercourses (Wasbauer, 1957).

Anoplius dreisbachi Evans. MOR-B, Aug. 1–15, 1 ♀, 2 ♂♂, ♀♂ on Per; HHS, July 17–30, 2 ♂♂.

Pompilus angularis (Banks). MOR-A, July 4–Aug. 14, 9 ♀♀, 3 ♂♂; ELK; Aug. 4–13, 2 ♀♀; PCR, Aug. 2, 2 ♀♀, 1 ♂; JAC, July 25, 1 ♂. Note nos. 1801, Aug. 1961, and 1986, July 12, 1964.

This species preys upon Salticidae (five records), Gnaphosidae (one record), and Thomisidae (one record) (Evans, 1959, 1963b; Wasbauer and Powell, 1962). It is a common species on sand flats along the Snake River. Number 1986 was dragging a spider (*Pellenes* sp. female) backward over the ground, grasping the base of the spider's hind legs in the common manner of Pompilidae. She ascended grass stems on several occasions, and at these times grasped one of the more anterior legs and dragged the prey up with its anterior end forward. She flew off from grass blades with her spider but gained little distance because of the weight of the prey. On one occasion she left the spider in a crotch 3 cm high while she searched about. The nest of the species has never been found.

Pompilus anomalus (Dreisbach). JAC, July 15, 1 ♂. Known to prey upon *Xysticus* (Thomisidae) (Wasbauer and Powell, 1962).

Pompilus occidentalis (Dreisbach). MOR, July 11–Aug. 8, 9 ♀♀, 13 ♂♂, ♀♂ on Per, Eri; ELK, Aug. 4–13, 2 ♀♀; PCR,

Aug. 13, 1 ♀; HHS, July 17–30, 5 ♀♀, 4 ♂♂. This species makes a short burrow in friable soil in wooded areas, provisioning the nest with *Pardosa* (Lycosidae) (Powell, 1957; Evans, 1963b).

Pompilus dakota (Dreisbach). MOR-B, July 16–Aug. 16, 8 ♀♀, 1 on Per; ELK, Aug. 4, 1 ♀; PCR, Aug. 2–13, 3 ♀♀.

Pompilus arctus Cresson. MOR-B, July 6–29, 1 ♀, 2 ♂♂, ♀ on Per; ELK, Aug. 4, 1 ♀, on Per; PCR, July 17–Aug. 2, 2 ♀♀, 2 ♂♂; HHS, July 17–30, 2 ♀♀. This species nests in a short burrow in sandy soil, usually in woodlands; the prey consists of Lycosidae, Gnaphosidae, Amaurobiidae, and Clubionidae (Evans and Yoshimoto, 1962).

Pompilus scelestus Cresson. MOR, PCR, HHS, ELK, common July 4–Aug. 26, chiefly on sandy soil, ♀♂ on Sol, Per, Eri. Note no. 2156, ELK, Aug. 16, 1967.

A female was seen at 1045 dragging a large spider backward across a sandy road. She circled about several times and then proceeded to the base of a sagebrush plant, where she placed the spider beneath the basal leaves of a nearby *Eriogonum* and dug into a burrow close to the base of the sagebrush. This burrow had evidently been previously prepared, as she soon came out and dragged the spider into the burrow and then made a rapid closure. She then began a new burrow only 5 cm away, at a 180° angle to the first burrow. She dug here for an hour before I captured her and dug out the first burrow. This burrow was nearly vertical and terminated in a cell at a depth of 3.5 cm. The spider had its anterior end uppermost, its legs forming a plug against which sand was packed; the egg had been laid transversely on the venter of the abdomen. Within two hours the spider had recovered fully from paralysis. It was preserved and found to be a female *Lycosa frondicola* Emerton. This species is known to prey upon Lycosidae in other parts of its range, also upon Pisauridae and Salticidae (Evans and Yoshimoto, 1962).

Pompilus fumipennis eureka (Banks). MOR-B, July 6–23, 2 ♀♀, 4 ♂♂, ♂ on Per; HHS, July 17–30, 6 ♀♀; ELK, Aug. 4–13, 1 ♀, 2 ♂♂; PCR, July 17, 1 ♂. This wasp is known to prey on Lycosidae (Evans, 1959; Wasbauer and Powell, 1962).

Pompilus apicatus Provancher. MOR-B, July 16–30, 4 ♀♀, 1 on Per; PCR, Aug. 2, 4 ♀♀; HHS, July 17–30, 4 ♀♀. Mainly a woodland species; prey and nesting behavior unstudied.

Aporinellus completus Banks. MOR-A, July 16, 1 ♀; JAC, July 15, 2 ♀♀. A predator on Salticidae (Evans and Yoshimoto, 1962).

Aporinellus taeniatus rufus Banks. MOR-A, July 14, 1 ♀, on sand. The nominate subspecies is known to prey upon Salticidae (Evans and Yoshimoto, 1962).

Family SPHECIDAE (Digger wasps)

Sphecidae made up nearly half of the wasp fauna of Jackson Hole (91 species as compared to 99 species in 11 other families together). Digger wasps are exceedingly diverse in their nesting and predatory behavior, as the following notes will testify. They are here considered by subfamily, in the following order: Sphecinae, Pemphredoninae, Astatinae, Larrinae, Crabroninae, Nyssoninae, and Philanthinae.

Subfamily SPHECINAE

Palmodes carbo Bohart & Menke. ELK, July 28–Aug. 16, 9 ♀♀, 2 ♂♂, ♀ on Per; 1 ♂, note no. 2032: taken as prey of *Philanthus zebratus nitens*; 3 ♀♀, note nos. 2125, 2143, 2156: nesting behavior.

Several females of this species nested somewhat gregariously in the middle of a sandy road ten meters from the Snake River, July 28–Aug. 16, 1967. The nests were in powdery, fine-grained sand among

short herbs and grass tufts; they were separated by 30–50 cm. Two prey taken from females or their nests proved to be large nymphs of *Cyphoderris monstrosa* Uhler, a long-horned grasshopper of the family Gryllacrididae; a third specimen, used for rearing a larva, was also evidently a nymph of this same species. These grasshoppers are nocturnal and spend the daylight hours resting under rocks and debris. They considerably exceed the wasps in size; one wasp 18 mm long was seen carrying a grasshopper 26 mm long and undoubtedly much heavier than herself. The hopper was straddled and carried forward, held by its antennae in the wasp's mandibles. One wasp climbed an herb 15 cm high with the prey, but the latter became entangled and had to be tugged free. The prey is evidently placed in or beneath a plant while the nest entrance is cleared of sand, the nest having been dug and closed before the initiation of hunting. When the closure has been removed, the wasp carries the prey to the threshold of the burrow, enters, and pulls in the prey by its antennae. The nest is then closed with rapid scraping movements of the front legs, only two to three minutes being required for closure. Only one grasshopper was used in each of the three nests excavated.

The nest is a short, oblique burrow 6–8 cm long, leading to a large, horizontal cell only 3–4 cm beneath the surface. The hopper is placed head-in, on its side, and the egg is laid at the base of the uppermost hind coxa, its anterior end fastened at or near the coxal membrane. The egg measures 4 mm in length. The larva feeds through the coxal membrane, hollowing out the inside by means of its slender anterior portion, reaching maturity in only six days and leaving the dismembered bits of the exoskeleton of the prey.

Palmodes hesperus Bohart & Menke. ELK, Aug. 4, 1 ♀; MOR-B, July 29–Aug. 3, 2 ♀♀, one on Sol, the other nesting, note no. 2134, Aug. 3, 1967.

A single female was seen closing a nest at 1415 in powdery sandy-loam a few meters from the riverbank (MOR-B2). She flew about in an excited manner, landing on various plants briefly and then returning to the nest. She picked up small stones and pieces of leaves and put them over the closed entrance. I caught the female and dug out the nest. The burrow was 7 cm long, reaching a horizontal cell 3 cm long and 5 cm beneath the surface. There was a single grasshopper in the cell, on its side, bearing the egg of the wasp in the same position as described for *P. carbo*. The prey was a large immature female of the Mormon cricket, *Anabrus simplex* Hald (Tettigoniidae). Bohart and Menke (1961) reported immatures of this same species as prey.

Podalonia communis (Cresson). MOR, July 3–Aug. 26, very common, ♀♂ on Sol; PCR, Aug. 13, 1 ♂; ELK, July 10–28, 1 ♀, 2 ♂♂, both males note no. 2126: taken as prey of *Philanthus zebratus nitens*. Nesting behavior, MOR-A2, July 24, 1967, note no. 2114.

Female seen digging in friable sand near river's edge at 1630 (Fig. 17). She dug for 20 minutes, producing a high-pitched buzzing sound. She then walked about ten meters away and seized a paralyzed cutworm (Noctuidae) which she had evidently hidden there. She carried it over the ground, straddling it and holding it with her mandibles; she deposited it about half way to the nest and returned to the nest by a circuitous route. After entering and leaving the nest, she returned to the cutworm and carried it to the entrance, then went in and pulled the prey in from the inside. As she approached the nest, she was followed by three very small miltogrammine flies (*Hilarella hilarella* Zett.), and at the same time a larger fly (*Metopia argyrocephala* Meigen) entered the empty nest and left again. After the wasp entered, all four flies perched on small herbs overlooking the nest. I left the area after

capturing the flies, and when I dug out the nest two days later I found several maggots which had destroyed the egg of the wasp. These were not reared to maturity.

Podalonia luctuosa (Smith). MOR, Aug. 10, 1 ♀; ELK, Aug. 9, 2 ♂♂, both note no. 2145: taken as prey of *Philanthus zebratus nitens.*

Podalonia mickeli Murray. MOR, July 16–Aug. 26, 2 ♀♀, one on Sol.

Podalonia occidentalis Murray. MOR, July 4–30, 1 ♀, 3 ♂♂.

Podalonia sericea Murray. MOR, July 16–Aug. 14, 4 ♀♀, 7 ♂♂, ♂ on Eri; ELK, Aug. 4–10, 3 ♀♀. Note no. 1791, MOR-B, Aug. 1, 1961; ♀ nesting along dirt road, preparing a very shallow nest which was provisioned with a single cutworm (Fig. 18). I reported on this under the incorrect name *P. robusta* (Evans, 1963b) and also described the larva under that name (Evans, 1964).

Podalonia sonorensis differentia Murray. MOR-B, July 8–30, 1 ♀, 1 ♂.

Ammophila azteca Cameron. MOR-A, July 7–Aug. 20, abundant; ELK, July 10–Aug. 2, 4 ♀♀, 8 ♂♂; HHS, July 13–Aug. 24, 1 ♀, 1 ♂. Note nos. 1993, 1996, 2007, 2012, 2013, 2018, 2028, 2029, 2030, 2031, 2046, 2050, MOR-A2, nesting behavior; note nos. 2032, 2131, 2133, ELK, 2 ♀♀, 1 ♂ taken as prey of *Philanthus zebratus nitens.*

This is one of the commonest wasps in sandy soil in Jackson Hole. It is the only North American digger wasp known to maintain several nests simultaneously. The burrows are vertical, 3–6 cm long, terminating in a horizontal cell 2.0–2.5 cm long. The prey consists of small larvae of sawflies or moths (Geometridae, Gelechiidae, rarely small Sphingidae); the prey is carried in flight. I have published a detailed study of this species elsewhere (Evans, 1965). (See also Figs. 19, 20, 31).

Ammophila cleopatra Menke. MOR, July 16, 1 ♀.

Ammophila dysmica Menke. MOR-B, Aug. 23, 1 ♀; ELK, July 28–Aug. 22, 1 ♀, 3 ♂♂. Note no. 2169, MOR-B, Aug. 23, 1967; note nos. 2124, 2133, ELK, July 28, Aug. 2, 1967: nesting behavior. Note no. 2133, ELK: 2 ♂♂ taken as prey of *Philanthus zebratus nitens.*

This species averages slightly larger than *azteca*, but preys on caterpillars of considerably larger size, carrying them over the ground rather than in flight. Number 2169 was carrying a striped noctuid caterpillar across a dirt road, pumping her abdomen up and down rapidly as if to gain momentum thereby. On reaching a patch of herbs at the roadside, she stopped and stung the caterpillar at several points on the venter (although it appeared well paralyzed) and then malaxated it just behind the head. Number 2124 was seen carrying a green noctuid caterpillar about the same length as the wasp; she also crossed a dirt road while pumping her abdomen up and down, then made a circuitous path through some herbs by the roadside and returned to the road vibrating her wings and moving rapidly over the ground, apparently unable to lift the caterpillar in flight. After covering about 15 meters she arrived at her nest in the center of the road, put the prey down, removed the closure, and drew in the caterpillar by its anterior end. In a few minutes she came out and began picking up lumps of earth and pushing them into the burrow while buzzing loudly. I dug out the nest at 1500, before she had finished filling, and found a single caterpillar in the cell with an egg on the side of the second abdominal segment. The burrow was vertical, the cell horizontal, only 3 cm deep. I believe this nest was receiving the final closure and that this one caterpillar was large enough to nourish the wasp larva.

Ammophila harti (Fernald). MOR-A, Aug. 25, 1 ♂, on Sol.

Ammophila macra Cresson. MOR-A, Aug. 14, 1 ♀; ELK, Aug. 13, 1 ♀. Note no. 2049, MOR-A2, Aug. 14, 1954. This very large species preys upon large sphingid larvae, using a single larva per nest (Fig. 20) (Evans, 1965).

Ammophila mediata Cresson. MOR-B, Aug. 23–26, 2 ♀♀, on Sol; ELK, Aug. 2, 1 ♀, note no. 2133: prey of *Philanthus zebratus nitens.*

[**Ammophila pilosa** (Fernald). South Gate, Yellowstone National Park, July 31, 1961, note no. 1785. Preys on small caterpillars, chiefly Lycaenidae, and stores several per cell (Evans, 1963b)].

Ammophila stangei Menke. MOR-B, July 16–30, 1 ♀, 2 ♂♂; JAC, July 25, 2 ♂♂.

Ammophila strenua Cresson. String Lake, Aug. 3, 1961, 1 ♂.

Subfamily PEMPHREDONINAE

Mimesa unicincta Cresson. MOR, July 12–Aug. 9, 3 ♀♀, 7 ♂♂, ♂ on Per; note no. 2127, MOR-B3: 1 ♂ taken as prey of *Philanthus pulcher.*

Mimumesa mixta (Fox). MOR, July 5–29, 1 ♀, 3 ♂♂; note nos. 1984, 2101, MOR-B3: 2 ♂♂ taken as prey of *Philanthus pulcher.* Species of this genus and the preceding are known to prey upon leafhoppers.

Diodontus argentinae Rohwer. ELK, July 28, 1 ♀; MOR-A, July 18–Aug. 17, 10 ♀♀, 4 ♂♂. Note nos. 2113, 2116: 1 ♀, 2 ♂♂, taken as prey of *Philanthus pulcher;* notes nos. 1991, 2004, 2161B: nesting behavior.

This is one of the most abundant wasps at MOR-A2, but I studied it only briefly. A large nesting aggregation occupied flat sand well back from the river and in well shaded areas among pine trees (Map 2). Burrow entrances were only about 1 mm in diameter; each hole had a small mound of sand (about 1 × 2 cm by 0.5 cm deep) in front of it. When digging the nest, females appear to move the front legs synchronously, but with little movement of the abdomen; the sand is thrown only a short distance, although the wasp backs out periodically and scrapes it away from the entrance. So far as I could determine, the nest entrance is left open at all times. Females emerge from their burrows head first and fly off swiftly, returning from time to time with an aphid held in their mandibles. The aphids were mainly wingless or subalate, occasionally fully winged. They were not identified, but it appeared that only one or a few species were involved.

Burrows are oblique, terminating in a succession of small cells at a depth of from 4 to 9 cm (Fig. 32). These cells are very small, each measuring about 2 × 4 mm, and are spaced 1–3 cm apart; the maximum number found per nest was five. Thirty or more aphids are packed very tightly into each cell and an egg is glued longitudinally along the venter of one of them. One of 13 cells excavated contained a dipterous maggot, but it was not reared successfully.

It should be added that *D. argentinae* has rarely been collected since its description. However, males were compared with the type specimen in the U. S. National Museum, and I feel that Rohwer's name properly applies to the species considered here. The American species of *Diodontus* have not been revised in many years, and identification of species is therefore difficult.

Diodontus ater (Mickel). MOR-B3, July 14–Aug. 26, 3 ♀♀, 3 ♂♂; note no. 2163: 1 ♂ taken as prey of *Philanthus pacificus*; note no. 2161A, 2172: nesting behavior.

In contrast to the preceding species, *D. ater* nested in sloping gravel banks at MOR-B3. The nest holes were left open, as in *argentinae*, and as in that species there was a small mound at the entrance of each nest. I dug out two nests and found one cell in each, at depths of 8 and

10 cm, but I may well have missed additional cells, as it was difficult to follow such small burrows in soil of this texture. The cells were provisioned with aphids very similar to those found in *argentinae* nests.

Diodontus gillettei Fox. ELK, July 10, 1 ♂; PCR, Aug. 13, 1 ♀; MOR, July 4–Aug. 17, 11 ♀♀, 8 ♂♂, several in trap; note nos. 1981, 2127: 4 ♂♂ taken as prey of *Philanthus pulcher*; note no. 2163: 2 ♀♀ taken as prey of *P. pacificus*.

Pulverro columbianus (Kohl). MOR-B, July 14–Aug. 3, 5 ♀♀, 8 ♂♂; 1 ♂ found in a spider web. This is the smallest digger wasp occurring in Jackson Hole, measuring only 3–4 mm in length. It was commonly seen flying around the ground at MOR-B2, but I was unable to locate any nests.

Pemphredon rileyi Fox. MOR, July, 1 ♀ in trap. [Also South Gate, Yellowstone National Park, Aug. 2, 1 ♀.]

Pemphredon tenax Fox. MOR, July 6–Aug. 4, 9 ♀♀, 1 ♂; JAC, July 25, 1 ♂. This is an aphid predator that nests in wood.

Stigmus americanus Packard. MOR, July, 1 ♀ in trap.

Passaloecus relativus Fox. ELK, Aug. 9, 1 ♀, note no. 2144: taken as prey of *Philanthus pacificus*; HHS, July 31–Aug. 11, 2 ♀♀; MOR-B, July 6–Aug. 23, 5 ♀♀, 3 ♂♂, note nos. 1981, 1992: 1 ♀, 1 ♂ taken as prey of *Philanthus pulcher*; also 1 ♂ taken as prey of the asilid fly *Laphria vivax* Williston.

Spilomena alboclypeata Bradley. MOR, July 18, 1 ♀.

Subfamily ASTATINAE

Astata bakeri Parker. MOR-B, Aug. 9, 4 ♂♂, all note no. 2037E: taken as prey of *Philanthus crabroniformis*.

Astata nubecula Cresson. MOR, July 16–Aug. 25, 5 ♀♀, 6 ♂♂, 1 ♂ on Eri; HHS, July 17–Aug. 11, 2 ♀♀, 1 ♂; ELK, 2–10 Aug., 2 ♀♀, 2 ♂♂; PCR, Aug. 13, 2 ♂♂. Note nos. 2032, 2133, ELK: 2 ♀♀ taken as prey of *Philanthus zebratus nitens*; note no. 2037E, MOR-B: 1 ♀ taken as prey of *Philanthus crabroniformis*. Note nos. 2105, 2121, 2140, 2166, 2175, MOR-B, July 18–Aug. 25, 1967: nesting and territorial behavior.

On July 27, two males were noted occupying perches some distance apart, one on low vegetation overlooking bare soil, another on a log about three meters from the river. The latter male occupied this perch for extended periods on three successive days, flying off in response to moving objects in the vicinity and returning quickly to resume an alert posture with antennae rigidly extended. Similar territorial behavior has been reported in other species of *Astata* (Evans, 1958).

Females nested in areas of bare, hard, stony soil. Nests were widely scattered, mostly in paths or along roads. Females spent several days (probably more than a week) at a nest, preparing several cells (maximum of eight found). Each nest had a small, splayed-out mound of soil at the entrance, which was closed between trips for prey. The burrow was oblique, leading to a group of cells, none of which appeared to be in series. The cells in five nests excavated varied in depth from 3 to 17 cm, but in any one nest the cells were of nearly the same depth (7.5 to 8.5 cm in the five cells of 2166, 10 to 12 cm in the eight cells of 2175). The cells each measured about 10×15 mm; the older cells in each nest appeared to be deeper than the ones prepared later. The nests were provisioned with immature stinkbugs (Pentatomidae); early in the season up to four small nymphs were used per cell, later in the season two or three larger ones. The bugs are placed in the smooth-walled cells venter-down, as in *A. unicolor* and *occidentalis* (Evans,

1958). They are carried to the nest in flight, the wasp holding the bug's antennae with its mandibles and also embracing it during flight with its legs (Fig. 8). The bug is deposited beside the nest entrance while the wasp scrapes it open. All of the more than 20 bugs taken from nests or from wasps belonged to one species, probably *Chlorochroa uhleri* Stål. One cell contained two maggots which formed their puparia a few days later and gave rise to two flies, *Senotainia trilineata* Wulp, in May, 1968. A fly captured in the field as it was trailing a prey-laden *Astata* proved to be *Hilarella hilarella* Zett.

Dryudella montana (Cresson). MOR-A, July 16–Aug. 18, 5 ♀♀, 1 ♂; PCR, Aug. 2, 1 ♀. Note no. 1782: MOR-A, July 30, 1961, nesting behavior.

This is a smaller wasp than the preceding. It nests in sandier soil and preys upon nymphs of Reduviidae, Scutelleridae, and Cydnidae. I have reported upon this species elsewhere (Evans, 1963b).

Subfamily LARRINAE

Plenoculus d. davisi Fox. MOR, July 7–Aug. 3, 8 ♀♀, 6 ♂♂; ELK. July 28–Aug. 9, 5 ♀♀. Note no. 2098, MOR-B3: taken as prey of *Philanthus pulcher*. Note nos. 1990, 2020B, 2115, 2138 (MOR), 2130, 2141 (ELK): nesting behavior.

This small wasp is abundant in Jackson Hole, nesting in friable soil in a variety of situations, both in areas A and B at MOR and along a sandy road at ELK. The burrow is only about 2 mm in diameter, but is fairly conspicuous because the entrance is usually left open and the mound unleveled. The upper part of the burrow is at an angle of about 30–45° with the surface, the lower part at a much steeper angle, often nearly 90°. The five nests excavated had from one to three cells each, the cells measuring about 4 × 6 mm and being from 5 to 8 cm deep.

The prey of this wasp consists of plant bugs (Miridae), both adults and immatures. The prey is carried to the nest in flight, often by short, hopping flights with frequent pauses, the wasp holding the bug's beak in its mandibles and embracing the body with its legs. The following mirids were taken as prey in the numbers indicated (in some cases the association of immatures with adults is uncertain):

Campylomma verbasci (Meyer)–1 adult, 7 immatures;
Orthotylus marginatus (Uhler)–1 adult;
Phylini (genus & spp. ?)–12 adults, 15 immatures;
Pilophorus amoenus Uhler–3 adults, 18 immatures.

The egg is about 1.5 mm long and is laid transversely on one of the bugs, one end attached behind a front coxa and the remainder extending off to one side of the bug. Kurczewski (1968) has provided a detailed account of the nesting behavior of this species. He found maggots in two nests, but I observed no parasitism in Jackson Hole.

Plenoculus propinquus Fox. MOR-A, July 31, 1 ♀, note no. 2020A: nesting behavior.

This species is very similar to the preceding, but may use somewhat larger prey and fewer per cell (Kurczewski, 1968). The one nest found at Jackson Hole had one cell, at a depth of 5 cm, containing three unidentified Miridae.

Solierella affinis (Rohwer). MOR, July 16–Aug. 26, 10 ♀♀, 4 ♂♂; note no. 2052: nesting behavior.

A female of this wasp was taken on August 16, 1964, entering an open hole with a bug of the genus *Nabis* (Nabidae). The burrow was 4 cm long and passed just beneath the surface, reaching a depth of only 1 cm; it may have been a pre-existing hole rather than one dug by the wasp. There were three more *Nabis* at the end of

the burrow; all four were last-instar nymphs, and actually exceeded the wasp slightly in length. Kurczewski (1967) has recently reviewed the biology of ground-nesting *Solierella*.

Solierella sayi (Rohwer). MOR, July 18–Aug. 26, 5 ♀♀, 3 ♂♂; ELK, Aug. 4, 1 ♀.

Nitelopterus cyanurus (Rohwer). MOR, July 16, 1 ♂.

Nitelopterus evansi Krombein. MOR, July 12–Aug. 22, 11 ♀♀, 16 ♂♂; JAC, July 25, 1 ♀, 1 ♂. Note nos. 1772, 1792, 2011, 2119, all MOR: nesting behavior.

I studied this very common, small wasp in some detail in 1961, and have already published an account of its biology (Evans, 1963b). Brief studies in 1964 and 1967 confirmed the fact that the prey consists exclusively of minute spiders of the genus *Dictyna* (Dictynidae). This is a minute wasp which spends much time flying about close to the ground (1–2 cm high) in the nesting area; during the morning hours males are often in the majority. The females dig their nests with synchronous strokes of the front legs and from time to time back across the mound of earth, keeping it fairly well dispersed. The entrance is kept closed much of the time. Each nest may have several cells (up to six found), the cells being only 2.5–5 cm deep. Provisioning females are often followed by satellite flies, *Senotainia trilineata*.

Pisonopsis c. clypeata Fox. MOR-B, July 11–Aug. 10, 6 ♀♀, 1 ♂; note nos. 2105, 2112, 2123: nesting behavior.

I have also published on the nesting behavior of this species (Evans, 1969). It is another predator on spiders, but utilizes small Theridiidae, including the whitish species *Chrysso nordica* (Chamberlin & Ivie) and two grayish species of *Theridion*, *rabuni* Chamberlin & Ivie and *petraeum* Koch (all females). One immature *Singa* (Araneidae) was taken from one nest. The nest is a shallow, pre-existing hole in the ground in which cells are prepared in series, separated by small lumps of earth which are picked up nearby and carried into the burrow. The cells are only 2–4 cm deep, each containing 9–17 spiders, the egg being laid obliquely on the dorsum of one of them. The burrow entrance is left open while the female provisions (Fig. 4).

Pisonopsis triangularis Ashmead. MOR, July 23, 1 ♀.

Trypoxylon aldrichi Sandhouse. MOR, July 11–Aug. 13, 3 ♀♀, 4 ♂♂; note nos. 1981, 2098: 3 ♂♂ taken from nests of *Philanthus pulcher*, MOR-B3.

Trypoxylon frigidum Smith. MOR, July 16–Aug. 3, 2 ♀♀, 1 ♂; PCR, Aug. 13, 1 ♀. Like the preceding, this is a twig-nester that preys upon spiders.

Larropsis capax (Fox). MOR, July 16–Aug. 3, 1 ♀, 2 ♂♂; ELK, Aug. 4–10, 2 ♀♀, 2 ♂♂, 1 ♂ note no. 2032: taken as prey of *Philanthus zebratus nitens*. [Also common at South Gate, Yellowstone National Park, July 19–Aug. 15, 26 ♀♀, 17 ♂♂.] This wasp is reported to use camel crickets (*Ceuthophilus* sp., immature) as prey. I saw females entering holes in the ground on two occasions, but found no nests.

Tachytes sayi Banks. MOR-B, Aug. 25, 1 ♀ on Sol.

Tachysphex aethiops Cresson. ELK, Aug. 4–13, 4 ♀♀, 1 ♂; HHS, July 13, 1 ♀; MOR, July 5–Aug. 1, 6 ♀♀, 8 ♂♂, ♀ on Eri. Note no. 2019, MOR-B3: 1 ♂ taken as prey of *Philanthus pulcher*; note no. 2051: nesting behavior, MOR-A2, Aug. 16, 1964.

On friable sand only two meters from the riverbank, a female was seen trying to enter a nest that had been stepped on. She was taken and the area excavated. An immature grasshopper, *Trimerotropis* sp.

(Acrididae), about 16 mm long, was located at a depth of 6 cm. A large mass of maggots was found on the prosternum, where they had evidently destroyed the egg of the wasp. This species evidently digs its own nest in flat, friable sand, as I observed several females digging, but I did not succeed in finding an active, undamaged nest.

Tachysphex nigrior Fox. MOR, July 16–30, 1 ♀, 2 ♂♂; note no. 2110: 2 ♂♂ taken from nest of *Philanthus pulcher*, as prey; note no. 2129: 1 ♀, nesting behavior, MOR-A1, July 30, 1967.

A female was observed walking rapidly over the sand with a grasshopper slung beneath her, the wasp holding the hopper by grasping its antennae with her mandibles. She entered a patch of grass, where the ground was covered with litter, and after making a few turns entered an open hole beneath a twig. There was a small mound of sand at the entrance. Five minutes later she was seen closing the nest, and I took her and dug out the nest. The shallow cell contained only the one grasshopper, which bore an egg transversely behind the front coxae. The hopper was an immature *Melanoplus* sp. (Acrididae) measuring 9.5 mm long (not counting the hind legs), approximately the same length as the wasp. The wasp had been followed all the way to the nest by a *Senotainia*, but I noted no maggots on the prey.

Tachysphex sp. near **linsleyi** Bohart. MOR-A, July 7–Aug. 15, 3 ♀♀, 4 ♂♂; note nos. 2002, 2093, 2153: nesting behavior.

A female was seen carrying a very small grasshopper over the sand at MOR-A1, on July 12, 1967, holding it in the manner described for *nigrior*. She was followed to her nest in a small pile of sand. I dug out the nest and found two cells side by side, about 1 cm apart, at a depth of 5 cm. One contained four very small grasshoppers, the other five; the egg of the wasp was found to be laid on the prosternum of the prey in the same manner as *nigrior*. The hoppers were all early instar *Melanoplus* sp. measuring about 4 mm long, considerably smaller than this small wasp. A second female was also taken with a small, immature *Melanoplus* on July 23.

A third female was noted at MOR-A2 on August 15 as she flew in to her closed nest entrance, holding the prey in flight with all three pairs of legs plus the usual grasp with the mandibles. She deposited the hopper at the entrance, opened the nest and went in, then came out and drew in the hopper by its antennae. I was able to find only one cell in this nest, at a depth of 3.5 cm, containing three immature grasshoppers 6–8 mm long, probably *Chloealtis conspersa* (Harris) (Acrididae).

Tachysphex tarsatus (Say). ELK, Aug. 4–10, 2 ♀♀; HHS, Aug. 11–24, 2 ♀♀; JAC, July 25, 1 ♀; MOR, 13 ♀♀, 20 ♂♂, July 4–Aug. 26, ♀♂ on Sol, Per; note nos. 2092, 2167: nesting behavior, MOR-A2, July 12–Aug. 22.

Females of this species were seen on several occasions carrying immature grasshoppers over the sand, holding the antennae of the prey with their mandibles as they straddled it. Some females moved their wings rapidly as if to gain added propulsion, but they did not lift their prey off the ground. One grasshopper, *Melanoplus* sp., measured 9.5 mm, about the same length as the wasp, while a second, probably *Trimerotropis* sp. measured 8 mm (both Acrididae). Females carrying prey often proceeded several meters over the sand, then circled about and plunged directly into the open nest entrance. The burrow is very short and evidently unicellular; the two nests excavated had a cell only 1–2 cm deep and each had only the one grasshopper. These brief observations are in accord with Williams' (1914) more detailed studies of this species, which were made in Kansas.

Tachysphex terminatus (Smith). ELK, Aug. 4, 1 ♀; PCR, Aug. 13, 1 ♀; MOR-A, July 4–Aug. 16, 5 ♀♀, 4 ♂♂; note nos. 2013, 2033: nesting behavior, MOR-A2, July 27–Aug. 5.

This species preys on small acridid grasshoppers and uses several per cell. The nest entrance is closed while the female is away. One of the two nests excavated had one cell at a depth of 3.2 cm, while the second had three cells at depths of from 4 to 4.5 cm (Fig. 30). The egg is laid across the venter of the prothorax in the usual manner of members of this genus. F. E. Kurczewski has been studying this species in detail in central New York. He has found species of *Melanoplus* to be used most commonly as prey. The mean length of the prey, based on some 900 specimens, was found to be about 6.8 mm, which is considerably less than the mean length of female wasps of this species (Kurczewski, 1966). I saved 20 prey grasshoppers from two nests in Jackson Hole; all were immature *Chorthippus curtipennis* (Harris) (Acrididae) measuring 5–9 mm (mean 6.5 mm).

Subfamily CRABRONINAE

Lindenius c. columbianus (Kohl). MOR, July 16–Aug. 16, 14 ♀♀, 7 ♂♂, ♀♂ on Per; ELK, Aug. 9, 1 ♀; JAC, July 25, 1 ♂. Note no. 2098, MOR-B, 1 ♀ taken from nest of *Philanthus pulcher*, as prey; note nos. 2047, 2144, MOR-A, 3 ♀♀, 1 ♂ taken from nest of *P. pacificus*, as prey; note no. 2053, MOR–B2, nesting behavior.

Despite the abundance of this minute species, I obtained few data on nesting behavior. Several nests excavated August 16, 1964, appeared to be incomplete. In each case the burrow was vertical, about 1.5 mm in diameter, the entrance surrounded by a rim of soil about 3 cm in diameter. One nest contained a single paralyzed chalcid wasp at a depth of 6 cm. This species is known to prey upon a variety of minute flies, bugs, and parasitic Hymenoptera (unpublished observations of author from other localities).

Crabro florissantensis Rohwer. ELK, July 10, 1 ♂; MOR-B, July 11, 1 ♂, note no. 1981: taken from nest of *Philanthus pulcher*, as prey.

Crabro largior Fox. ELK, July 28, 1 ♀.

Crabro latipes Smith. MOR, July 7–Aug. 18, 4 ♀♀, 10 ♂♂, ♀♂ on Per; HHS, July 31–Aug. 24, 6 ♀♀; ELK, Aug. 2–13, 2 ♀♀, 2 ♂♂, 1 ♂ note no. 2131: taken as prey of *Philanthus zebratus nitens*. Like other members of the genus, this is a ground-nester which preys upon flies.

Crabro pleuralis Fox. ELK, Aug. 16, 1 ♀, note no. 2155: taken from nest of *Philanthus zebratus nitens*, as prey.

Crossocerus maculiclypeus (Fox). MOR-A, July 11, 1 ♀; PCR, Aug. 13, 1 ♀, 1 ♂; ELK, Aug. 16, 1 ♀, note no. 2159; taken as prey of *Philanthus pacificus*. Note no. 1983, MOR-A1, July 11, 1964: nesting behavior.

A female was seen at 1030 plunging into an open nest entrance two meters from the bank of the Snake River. Her abdomen was held very high, at an angle to the remainder of the body, and she held prey beneath her thorax, probably by the middle legs. The burrow entrance was only 1.5 mm in diameter and there was no evidence of a mound of fresh earth around it. This nest was dug out an hour later and found to contain six cells. The cells were small, each about 2×4 mm, and all were between 6 and 7.5 cm deep, spaced about 1 cm apart. Each cell contained numerous small flies (18 in the one cell counted), the majority small acalyptrates (List 3). Several cells contained an egg of the wasp, in each case attached to the "throat" of the fly (ventrally, between the head and

front coxae) and extending laterad at a right angle to the body of the fly. Two larvae were reared to maturity and preserved for future study.

LIST 3

Prey Records for *Crossocerus maculiclypeus* (Fox), Jackson Hole, Wyoming

CHIRONOMIDAE
Cricotopus sp. 1
Genus and species? 1

EMPIDIDAE
Bicellaria pectinata Mel. 2
Platypalpus cellarius Mel. 1
Platypalpus xanthopodus Mel. 1

AGROMYZIDAE
Liriomyza sp. 1
Melanagromyza sp. 6

PSILIDAE
Psila rosae Fabr. 1

EPHYDRIDAE
Hydrellia sp. 3

CHLOROPIDAE
Chlorops sp. 1
Conioscinella melancholica Beck 1

MUSCIDAE: COENOSIINAE
Genus and species? 1

Crossocerus nigricornis (Provancher). MOR, July 29, 1 ♀. This species also preys upon various small flies, but nests in hollow stems (Pate, 1944).

Crossocerus wickhamii (Ashmead). MOR, July 13–Aug. 17, 6 ♀♀, 2 ♂♂, ♀♂ on various Umbelliferae; HHS, July 31, 1 ♀. Also nests in cavities in wood, but preys upon leafhoppers (Steyskal, 1944).

Ectemnius chrysargyrus (Lepeletier & Brullé). MOR-B, July 27–Aug. 26, 5 ♀♀, 3 ♂♂, ♀♂ on Sol, ♂ on Eri; HHS, July 23, 1 ♀. Like many of its congeners, this species nests in cavities in wood and preys upon flies.

Ectemnius continuus (Fabricius). MOR-B, July 7–Aug. 14, 5 ♀♀, 6 ♂♂; HHS, Aug. 24, 1 ♀.

Ectemnius corrugatus (Packard). MOR, July 7, 1 ♀, 1 ♂.

Ectemnius d. dilectus (Cresson). MOR-B, Aug. 1–26, 3 ♀♀, 3 ♂♂, all on Sol.

Ectemnius dives (Lepeletier & Brullé). MOR-B, July 6–Aug. 19, 6 ♀♀, 2 ♂♂, ♀ on Sol, Per; Note no. 2019, ♂ taken as prey of *Philanthus pulcher*.

Ectemnius lapidarius (Panzer). MOR-B, July 6–Aug. 26, 4 ♀♀, 1 ♂, ♀ on Sol; ELK, July 1–Aug. 10, 2 ♂♂.

Ectemnius nigrifrons (Cresson). MOR-B, July 7–Aug. 23, 1 ♀, 3 ♂♂, ♀ on Sol.

Ectemnius spiniferus (Fox). MOR, July 7, 1 ♂.

Ectemnius trifasciatus (Say). ELK, Aug. 4, 1 ♀; JAC, July 25, 1 ♀.

Lestica interrupta bella (Cresson). MOR-B, Aug. 1–26, 8 ♀♀, 10 ♂♂, ♀♂ on Sol, Per; JAC, July 25, 1 ♂. Nests in logs; the nominate subspecies is known to prey upon small moths (Peckham & Peckham, 1905).

Belomicrus f. forbesii (Robertson). PCR, Aug. 2, 1 ♀; MOR, July 4–Aug. 26, 8 ♀♀, 12 ♂♂, ♀ on Sol. Note nos. 2019, 2110, 2116: 2 ♀♀, 6 ♂♂, all taken as prey of *Philanthus pulcher*, MOR-B3. Note no. 2111, nesting behavior, MOR-B3, July 22, 1967.

This species was found nesting within the limits of an aggregation of *Philanthus pulcher*, which not infrequently uses it as prey. The female *Belomicrus* digs an oblique burrow by flying upward and backward periodically and dropping the soil on the ground some distance from the burrow. The one nest studied had a burrow about 10 cm long; there were four cells at a depth of about 6 cm, each provisioned with

immature or adult mirid bugs, apparently all *Orectoderus obliquus*. Two of the cells contained parasitic maggots, and from these, two adult flies (*Senotainia trilineata* Wulp) were reared the following spring. A fly of this same species was captured at the nest entrance of the wasp. A fuller report on the nesting behavior of *Belomicrus forbesii* has been presented elsewhere (Evans, 1969).

Oxybelus emarginatus Say. MOR-A, July 16–28, 3♂♂. This is a ground-nesting wasp that preys on midges and other small Diptera (Krombein and Kurczewski, 1963).

Oxybelus uniglumis quadrinotatus Say. MOR-A, July 4–Aug. 26, abundant, ♀♂ on Sol; ELK, Aug. 4, 1 ♀; HHS, Aug. 11, 1 ♀; JAC, July 25, 1 ♀; PCR, Aug. 2, 1 ♀, 1 ♂. Note no. 2098: 6 ♂♂ taken from nests of *Philanthus pulcher*, as prey, MOR-B3. Note nos. 1818, 2090, 2095, 2100, 2103, 2104, 2150: nesting behavior, MOR-A1, A2, July 10–Aug. 11, 1961, 1967.

There are many published reports on the nesting behavior of this widely distributed species, and I shall present only a few notes here. The nests are dug in light, friable sand by very rapid strokes of the front legs while the wasp's body is nearly perpendicular to the ground. The burrow is oblique, only about 4 mm in diameter, the soil from the burrow being allowed to remain in a small mound at the entrance. In the several nests studied, burrow length varied from 6 to 10 cm, cell depth from the surface directly above from 4 to 7 cm; the cells are small, measuring about 5 × 8 mm. In this locality the number of cells per nest varied from one to four; when more than one cell is constructed per nest, the cells are closely clustered, separated by no more than 0.5–1.0 cm (Fig. 26).

The prey is carried on the sting, which is thrust into the thorax of the fly, permitting the wasp to stand on all three pairs of legs while opening the nest entrance. In Jackson Hole, the prey consisted of various medium-sized flies, particularly blood-sucking Rhagionidae of the genus *Symphoromyia* and various Muscidae and Anthomyidae (List 4). Many other flies taken from nest-cells, but not saved for identification, appeared to represent these same or related species. From four to eight flies are used per cell. The egg is laid across the throat of one of the flies as usual in this genus.

Several females carrying prey were seen to be followed by miltogrammine flies (*Senotainia trilineata* Wulp). Three of 15 cells excavated contained maggots. The contents of all three cells were reared successfully; two produced adult *Senotainia trilineata*, the third a single adult *Phrosinella fulvicornis* (Coq.).

LIST 4

Prey records for *Oxybelus uniglumis quadrinotatus* Say, Jackson Hole, Wyoming

RHAGIONIDAE
Symphoromyia atripes Bigot 5
Symphoromyia montana Aldrich 4

LAUXANIIDAE
Sapromyza monticola Melander 1

ANTHOMYIDAE
Hylemyia depressa Stein 6
Hylemyia lasciva Zett. 1
Hylemyia platura Meigen 2

MUSCIDAE
Myospila meditabunda Fabr. 2
Spilogona sp. 7

TACHINIDAE
Eulasiona comstocki Townsend 1

Subfamily NYSSONINAE

Alysson radiatus Fox. MOR, July 4, 1 ♂. Members of this genus and the following prey upon leafhoppers and related insects and nest in the ground, often in damp or shaded situations.

[**Didineis nodosa** Fox. South Gate, Yellowstone National Park, Aug. 2, 1 ♂.]

Ochleroptera bipunctata (Say). JAC, July 25, 2 ♂♂. Known to prey on a variety of small Homoptera (see Evans, 1966a, pp. 75–77).

Gorytes albosignatus Fox. ELK, Aug. 4, 1 ♀.

Gorytes canaliculatus asperatus Fox. MOR-A, July 15–Aug. 14, 8 ♀♀; note nos. 1802, 1995, 2044, 2097: nesting behavior.

This species nests in fine-grained sand within a few meters of the Snake River; the nest is an oblique burrow with one or more terminal cells. The prey consists of leafhoppers, principally of the genus *Idiocerus*. In Jackson Hole the two species employed were *I. apache* Ball & Parker and *I. perplexus* Gillette & Baker. Data gathered in 1961 and 1964 have already been published (Evans, 1966a, 1968). The one nest dug out in 1967 was unicellular and very shallow, a burrow 8 cm long terminating in a cell 6 cm deep. Provisioning females were seen to be followed by miltogrammine flies, *Senotainia trilineata* Wulp, and one fly, *Metopia argyrocephala* (Mg.) was reared from a nest.

Hoplisoides spilographus (Handlirsch). MOR, July 12–Aug. 5, abundant; note nos. 1988, 1994, 1998, 2006, 2017, 2094, 2102: nesting behavior.

This species nests in coarser soil than the preceding, often in heavy clay-loam with many stones. The nest is similar to that of the preceding species (Fig. 28), but the prey consists of Membracidae, in Jackson Hole always of a single species of immature Ceresini. I obtained many more prey records in 1967 beyond those reported earlier (Evans, 1966a: 46–49), and all represented this same treehopper. This species was unusually common in 1967, and I found two dense nesting aggregations, each of 20 or more females, the nests sometimes separated by only a few centimeters. *Nysson rusticus* Cresson, reported as a possible parasite in 1966, was in 1967 actually seen digging into a *Hoplisoides* nest entrance. The flies *Senotainia trilineata* (Wulp) and *S. rubriventris* Macq. were also seen following provisioning females.

[**Hoplisoides spilopterus** (Handlirsch). South Gate, Yellowstone National Park, July 19, 1 ♀].

Dienoplus pictifrons Fox. MOR, July 11–Aug. 14, 7 ♀♀, 16 ♂♂, ♂ on Per; ELK, Aug. 4, 1 ♀; HHS, Aug. 11, 1 ♀. Note nos. 1981, 1984, 1992, 2116, all MOR-B, 1 ♀, 14 ♂♂: all taken as prey of *Philanthus pulcher*.

Nysson daeckei Viereck. MOR, July 12–Aug. 12, 3 ♀♀; ELK, July 10, 1 ♀. Note no. 2091Z, MOR-B, July 12, ♀ seen flying from one nest entrance of *Philanthus pulcher* to another, but not seen entering any nests. This is a known parasite of *Gorytes* and *Hoplisoides* and was probably attacking members of these genera, which nested in the area.

Nysson rusticus Cresson. MOR, July 7–Aug. 19, 7 ♀♀, 4 ♂♂; note nos. 1994X, 1998, 2094; several ♀♀ taken in close association with *Hoplisoides spilographus* nests, one seen entering a nest.

Nysson simplicicornis Fox. MOR, July 12, 1 ♀.

Stictiella emarginata (Cresson). MOR, July 14–Aug. 26, 4 ♀♀, 10 ♂♂, ♀♂ on Sol, ♂ on Eri. Although this is one of the larger and more common wasps in Jackson Hole, I was unable to find it nesting; the prey is reported to consist of adult moths (Noctuidae) (Gillaspy, Evans, and Lin, 1962).

Steniolia obliqua (Cresson). MOR, July 10–Aug. 26, abundant, ♀♂ on Sol, Erigeron; ELK, Aug. 4, 1 ♀. Note no. 2162,

Aug. 17, 1967, plus extensive notes taken in 1961 and 1964, summarized by Evans and Gillaspy (1964) and Evans (1966a).

This species forms massive "sleeping clusters," chiefly on low branches of lodgepole pine, and the females make shallow nests in fine-grained, powdery sandy loam at some distance from the clusters. The prey consists almost entirely of flies of the family Bombyliidae. Studies during 1964 and 1967 confirmed the fact (pointed out in Evans and Gillaspy, 1964) that species of the bombyliid genus *Villa* make up about 80 per cent of the prey (*V. sinuosa jannickeana* O. S., *V. l. lateralis* Say being used in considerable numbers, *V. alternata* Say and *V. concessor* Coq. in small numbers). Other flies used include the bombyliids *Geron* sp. and *Bombylius* sp., and the syrphid *Pipiza calcarata* Lowe. Natural enemies include the chrysidid wasp *Parnopes edwardsii* (Cresson) and the flies *Taxigramma heteroneura* (Mg.) and *Hilarella hilarella* (Zett.), but the flies were not shown to develop successfully in the cells of this species. Further details on the biology of this species may be found in the references cited above. (See also Figs. 5, 15, 16, 25.)

Bembix americana spinolae Lepeletier. MOR-A, July 18–Aug. 26, abundant, ♀ ♂ on Sol; ELK, July 10–Aug. 13, abundant; HHS, July 23–Aug. 24, abundant. Note nos. 1793, 1820, 1987, 2005, 2009, 2010, 2014, 2043, 2107, 2122, 2168 (MOR-A2); 2142, 2158 (ELK); 2168A (HHS): all nesting behavior, summarized in part by Evans (1966a).

This species is largely restricted to certain areas of fine-grained alluvial sand. A large nesting aggregation occurred each summer at MOR-A2 and at ELK, in both cases close to the river; at HHS an aggregation of about 50 wasps occupied a sandy road through a meadow. The nest is a simple oblique burrow with a terminal cell (Figs. 9, 24). There was no significant difference in nest depth at the three localities; pooled data on 21 nests showed a burrow length of from 10 to 20 cm (mean 16 cm), cell depth of from 5 to 11 cm (mean 8). Parasites include the conopid fly *Physocephala texana* Will., which attacks the adults, and the miltogrammine fly *Senotainia trilineata* (Wulp); one of the latter was reared from a maggot found in a cell also containing a healthy, nearly full-grown *Bembix* larva. Other probable parasites include the chrysidid *Parnopes edwardsii* (Cresson) and the bombyliid fly *Exoprosopa dorcadion* O. S.

During 1964 deerflies were unusually abundant in area 2 at Moran, and these wasps preyed extensively upon them (*Chrysops furcatus* Walker and *C. noctifer pertinax* Will.). In 1967 these flies were relatively uncommon, and a wide variety of other flies was employed. In the three localities during the three summers of study, no less than 43 species of flies were employed as prey (List 5).

Bembix amoena Handlirsch. HHS, July 31, 1 ♀. This species is abundant in Yellowstone, nesting in coarse geyserite near hot springs and geysers (Evans, 1966a: 269–288). It preys upon a wide variety of flies. I have never taken this species within Grand Teton National Park.

LIST 5

Flies employed as prey by *Bembix americana spinolae* in Jackson Hole, Wyoming

Species of fly	*No. taken 1964*	*No. taken 1967*
STRATIOMYIDAE		
Odontomyia hoodiana Bigot	1	
TABANIDAE		
Chrysops furcatus Walker	25	
C. noctifer pertinax Will.	20	
C. mitis O. S.	2	
Hybomitra osburni Hine	1	
H. phaenops O. S.	2	

BOMBYLIIDAE		
Conophorus painteri Priddy	1	
Systoechus fumipennis Painter	1	
Villa agrippina O. S.	1	
V. alternata Say	1	2
V. fulviana Say	1	
V. sinuosa jaennickiana O. S.	1	2
THEREVIDAE		
Thereva cingulata Kroeb		6
ASILIDAE		
Lasiopogon cinereus Cole	1	
Tolmerus callidus Will.		6
DOLICHOPODIDAE		
Dolichopus crenatus O. S.	1	
Dolichopus procerus VanD.	1	
SYRPHIDAE		
Chrysotoxum ventricosum Loew	1	
Dasysyphus amalopsis O. S.	1	
Eupeodes volucris O. S.	1	
Helophilus obscurus Loew	1	
H. latifrons Loew		2
Melanostoma sp.	2	
Metasyrphus palliventris Curran	1	
M. astutus Fluke		2
Microdon lanceolatus Adams	1	
Paragus bicolor Fabr.	1	
Scaeva pyrastri L.	3	
Sphaerophoria sp.	1	1
Syrphus opinator O. S.	8	1
S. ribesii L.	2	1
Xylota bigelowi Curran		2
SCIOMYZIDAE		
Renocera quadrilineata Mel.	1	
Tetanocera plumosa Loew		1
ANTHOMYIDAE		
Cordilura latifrons Loew	3	
Hydrophoria divisa Mg.	1	
Hylemyia sp.		1
MUSCIDAE		
Helina cinerella Wulp	2	1
Helina latifrons Zett.		2
Helina troene Walk.		1
Pyrellia serena Mg.	1	
Quadrularia annosa Zett.	1	
Spilogona sp.	1	
CALLIPHORIDAE		
Eucalliphora lilaea Wlk.	1	
Lucilia sp.		1
Phormia regina Mg.		1
TACHINIDAE		
Bonellimyia glauca Brks.		4
Dinera sp.		3
Microphthalma disjuncta Wied.		1
Nearchus duplaris Reinh.	1	
Ptilodexia sp.		1
Trochilodes skinneri Coq.		1

Subfamily PHILANTHINAE

Aphilanthops subfrigidus Dunning. MOR, Aug. 8, 1 ♂, on Sol; PCR, Aug. 2, 1 ♂; ELK, July 28–Aug. 13, 5 ♀♀, 4 ♂♂, note nos. 2126, 2133: 5 ♂♂ taken as prey of *Philanthus zebratus nitens*; note no. 2041: nesting behavior.

This species was found nesting in small numbers in the center of a hard dirt road at ELK on August 13, 1964. Each nest entrance had a small, well-scattered mound of soil at the entrance; the nest entrance appeared to be left open while females were hunting. Females returning with prey were often followed by miltogrammine flies (*Senotainia trilineata* Wulp), and other flies (*Metopia argyrocephala* Mg.) perched at nest entrances. One burrow was traced to 10 cm, where there was a storage cell containing six queen ants, all with intact wings. All appeared to be *Formica neogagates* Emery. A search was made for brood cells without success.

Philanthus pulcher Dalla Torre. MOR, July 8–Aug. 3, abundant, ♀♂ on Eri, Sol; ELK, July 28, 1 ♀; HHS, July 23, 1 ♀; JAC, July 15, 3 ♀♀; PCR, Aug. 2, 3 ♀♀. Note nos. 1981, 1982, 1984, 1992, 2019, MOR-B, July 11–31, 1964; note no. 2089, ELK, July 10, 1967; note nos. 2091, 2096, 2098, 2101, 2109, 2110, 2113, 2116–2118, 2127, 2160, MOR-B, July 11–29, 1967: all nesting behavior. I have already published briefly on this species (Evans, 1966c), and I hope to present a detailed comparative study of the species of *Philanthus* elsewhere. Only a few remarks on nests and prey are presented here.

This species forms dense nesting aggregations in areas of more or less bare,

moderately hard-packed clay-loam. It is an early season species, beginning its nesting activity in early July and extending into the first few days of August (1964) or until July 30 (1967). Nests are often separated by only a few centimeters, and each female makes a series of nests in the same general area, each nest occupying about seven to ten days of her life. During this time several cells are prepared, the maximum number found in one nest being six. The 49 cells excavated varied in depth from 6 to 10 cm (mean 8.3 cm). The number of prey per cell varied from 6 to 14, cells with smaller prey usually containing more specimens. A few cells contained nothing but wasps, many all bees, while the majority contained a mixture of wasps and bees, often several species mixed; on the whole, bees were slightly more plentiful than wasps in the cells, although about equal numbers of species of the two groups were utilized (List 6). I presented some preliminary notes on digging, leveling, and closure in 1966, and hope to cover these matters in more detail in a future paper. (See Figs. 10, 12, 36, 37.)

LIST 6

Prey records for *Philanthus pulcher* D. T., Jackson Hole, Wyoming

WASPS

71 records, 25 species

SCELIONIDAE
- *Scelio* sp. 1♀

CHRYSIDIDAE
- *Chrysura pacifica* Say 1♂
- *Elampus viridicyaneus* Norton 1♂
- *Hedychridium fletcheri* Bod. 1♀, 3♂♂
- *Holopyga ventralis* Say 1♀
- *Omalus aeneus* Fabr. 1♀

EUMENIDAE
- *Ancistrocerus catskill* Saussure 1♂
- *Stenodynerus papagorum* Viereck 1♀, 1♂
- *Symmorphus canadensis* Saussure 1♀

SPHECIDAE
- *Belomicrus forbesii* Robt. 2♀♀, 6♂♂
- *Crabro florissantensis* Roh. 1♂
- *Dienoplus pictifrons* Fox 1♀, 14 ♂♂
- *Diodontus argentinae* Rohwer 1♀, 2♂♂
- *Diodontus gillettei* Fox 4♂♂
- *Ectemnius dives* Lep. & Br. 1♂
- *Lindenius columbianus* Kohl 1♀
- *Mimesa unicincta* Cresson 1♂
- *Mimumesa mixta* Fox 2♂♂
- *Passaloecus relativus* Fox 1♀, 1♂
- *Plenoculus davisi* Fox 1♀
- *Oxybelus uniglumis quadrinotatus* Say 6♂♂
- *Tachysphex aethiops* Cresson 1♂
- *Tachysphex nigrior* Fox 2♂♂
- *Tachysphex* sp. 2♀♀, 7♂♂
- *Trypoxylon aldrichi* Sandh. 3♂♂

BEES

98 records, 23 species

COLLETIDAE
- *Colletes nigrifrons* Titus 3♂♂
- *Hylaeus basalis* Smith 5♀♀
- *Hylaeus conspicuus* Metz 2♂♂
- *Hylaeus ellipticus* Kirby 1♀, 4♂♂

ANDRENIDAE
- *Andrena melanochroa* Ckll. 1♀
- *Panurginus atriceps* Cresson 7♀♀, 3♂♂
- *Panurginus cressoniellus* Ckll. 3♂♂
- *Perdita wyomingensis* Ckll. 2♂♂

HALICTIDAE
- *Dialictus laevissimus* Smith 17♀♀
- *Dialictus ruidosensis* Ckll. 1♀
- *Dialictus* spp. 27♀♀
- *Dufourea maura* Cresson 1♀
- *Dufourea scabricornis* Bohart 1♂
- *Evylaeus niger* Viereck 1♀
- *Halictus confusus* Smith 2♀♀
- *Halictus tripartitus* Ckll. 3♀♀
- *Sphecodes* sp. 2♀♀

MEGACHILIDAE
- *Formicapis clypeata* Sladen 2♀♀
- *Hoplitis producta* Cresson 1♂
- *Osmia pentstemonis* Ckll. 1♀
- *Osmia* spp. 2♂♂
- *Stelis lateralis* Cresson 1♂

ANTHOPHORIDAE
Nomada spp. 5♂♂

On many occasions, provisioning females were seen to be followed by female *Senotainia trilineata* Wulp, and on several occasions apparent successful larviposition on the prey was observed, usually as the wasp was about to enter the nest. A larger fly, *Phrosinella pilosifrons* Allen, was also commonly seen digging at closed nest entrances, and one fly of this species was reared from a cell (emerging in May, 1968, from a cell provisioned in July, 1967). On a number of occasions cuckoo wasps, usually *Hedychridium fletcheri* Bod., but on one occasion *Ceratochrysis trachypleura* Bohart, were seen flying from one nest entrance to another but not actually entering; once a *Senotainia* was seen following a *Hedychridium* for a minute or two! A female *Nysson daeckei* Viereck was also seen flying from one nest entrance to another.

Philanthus crabroniformis Smith. MOR-B, July 22–Aug. 26, abundant. ♀♂ on Sol, ♂♂ on *Achillea*; HHS, Aug. 24, 1 ♀, 1 ♂; JAC, July 25, 1 ♀. Note nos. 2037, 2040, 2045, MOR-B, Aug. 8–14, 1964; note nos. 2128, 2135, 2136, 2139, 2147, 2148, 2152, 2154, 2164, 2165, 2171, 2173, 2174, 2176, MOR-B, July 29–Aug. 26, 1967; note nos. 2149, 2171A, HHS, Aug. 11, 1967: all nesting behavior.

This species forms rather diffuse nesting aggregations in hard, stony soil, nest entrance sometimes separated by 10–30 cm, but more often separated by a meter or more. Rarely I have found *pulcher* and *crabroniformis* occupying the same bare area; much more commonly *pulcher* is to be found in appreciably more sandy and less stony soil. There is virtually no seasonal overlap. In 1967 the first male *crabroniformis* appeared on July 22, and females were seen digging on July 24. However, digging of the nest takes several days, and no prey carriage was observed until August 1, two days *after* the last *pulcher* was seen with prey. In contrast to *pulcher*, this species does not level the mound of soil at the nest entrance except in an irregular and incomplete manner; but at least half the nests have (at some time) one or two accessory burrows beside the true nest entrance, which is kept closed when the female is hunting. Also in contrast to *pulcher*, females usually maintain a single nest for the duration of their lives, making as many as 15 cells, and probably more (Fig. 38). The first cells are constructed closest to the entrance, and as the season progresses the burrow is lengthened and additional cells constructed on each side of the burrow progressively farther from the entrance. The final burrow length may be 70 cm or more; in any one burrow the cells tend to be at about the same depth (13–16 cm in the 15 cells of no. 2173; 9–15 cm in the 13 cells of no. 2165; range of variation of all cells 9–21 cm). The cells measure about 12 × 22 mm and are provisioned with from 12 to 24 small bees or wasps, the egg being laid on the top of the pile in the usual manner of wasps of this genus. Although this is a larger species than *pulcher*, it takes very small prey and only rarely uses wasps; about three-fourths of the 386 prey taken from nests or from wasps consisted of a single species of *Dialictus* (List 7).

LIST 7

Prey records for *Philanthus crabroniformis* Smith, Jackson Hole, Wyoming

WASPS

6 records, 3 species

SPHECIDAE
Astata bakeri Parker 4♂♂
Astata nubecula Cresson 1♀
Plenoculus davisi Fox 1♀

BEES

380 records, 16 species

COLLETIDAE
Hylaeus sp. 2♀♀

ANDRENIDAE
Andrena albosellata Ckll. 1♀
Andrena sp. 3♀♀
Perdita fallax Ckll. 2♀♀

HALICTIDAE
Dialictus laevissimus Smith 47♀♀, 243 ♂♂
Dialictus sp. 6♀♀, 17♂♂
Evylaeus cooleyi Cwfd. 1♂
Evylaeus niger Viereck 1♀, 5♂♂
Evylaeus peraltus Ckll. 2♂♂
Evylaeus synthyridis Ckll. 1♀, 2♂♂
Halictus confusus Smith 1♀, 6♂♂
Halictus tripartitus Ckll. 4♀♀
Halictus rubicundus Christ 1♀, 6♂♂
Sphecodes patruelis Ckll. 12♂♂
Sphecodes sulcatulus Ckll. 2♂♂
Sphecodes spp. 15♂♂

This species was attacked by much the same parasites as *pulcher*, these parasites simply shifting their attention from one species to the other as the season progressed. Many provisioning females were followed by *Senotainia trilineata* Wulp, and two flies of this species emerged in May 1968 from cells collected in August 1967. *Phrosinella pilosifrons* Allen was also very commonly seen digging at closed nest entrances, and several of these were also reared from cells (Fig. 14). *Metopia argyrocephala* Mg. was observed following females and entering nests and accessory burrows, but I did not rear this species. Female *Ceratochrysis trachypleura* Bohart were seen on several occasions flying from one nest entrance to another. The flight patterns of prey-laden females followed by satellite flies have been described in an earlier section.

Philanthus zebratus nitens (Banks). ELK, July 28–Aug. 16, abundant; HHS, July 23–31, 3 ♀♀, 10 ♂♂; JAC, July 15, 1 ♂. About a third of the females collected have yellowish abdominal markings, and will thus key to *z. zebratus* Cresson, a form of more southerly distribution than *nitens*; I question the value of these subspecific names. Note nos. 2032, 2036, 2131, 2132, 2133, 2145, 2146, 2155, all ELK: nesting behavior. Evans (1966c) discussed this species briefly.

This species was never taken at MOR, but was common along a sandy road at HHS; all studies were made on a very large colony of approximately 200 females nesting in or near a sandy road at ELK. This is a large, colorful species which makes conspicuous nest holes and preys on relatively large bees and wasps. The nests are similar in structure to those of *crabroniformis*, cells being constructed on either side of a burrow that is progressively lengthened (Fig. 39). As many as 17 cells may be made per nest, and some females, at least, appear to maintain a single nest for their life of about a month. Cell depth varies from 8 to 18 cm and is sometimes that variable within one nest, although in others all cells are at nearly the same depth (13–16 cm in the 11 cells of no. 2132). Cells measure about 12 × 20 mm and contain from three to nine (usually four to seven) fairly large bees or wasps. The mound of earth at the nest entrance tends to be somewhat spread out, but it is not leveled; a small percentage of nests have one or two (rarely three) accessory burrows. The nest entrance is usually closed while the female is out. Prey records are summarized in List 8.

LIST 8

Prey records for *Philanthus zebratus nitens* (Banks), Jackson Hole, Wyoming

WASPS

75 records, 25 species

ICHNEUMONIDAE
Diphyus sp. 4♂♂
Dusona sp. 1♀
Eutanyacra sp. 1♀, 1♂
Ichneumon sp. 12♂♂
Spilichneumon sp. 2♀♀, 8♂♂

EUMENIDAE
Ancistrocerus adiabatus Sauss. 1♀, 1♂
Euodynerus castigatus Sauss. 1♂
Stenodynerus taos Cresson 1♀
Symmorphus meridionalis Viereck 1♀

MASARIDAE
Pseudomasaris edwardsii Cresson 1♂

SPHECIDAE
Ammophila azteca Cameron 3♀♀, 2♂♂
Ammophila dysmica Menke 2♂♂
Ammophila mediata Cresson 1♀
Aphilanthops subfrigidus Dunning 5♂♂
Astata nubecula Cresson 2♀♀
Cerceris aequalis idahoensis Scullen 1♀
Crabro pleuralis Fox 1♀
Crabro latipes Smith 1♂
Ectemnius sp. 2♀♀
Eucerceris fulvipes Cresson 2♂♂
Larropsis capax Fox 1♂
Palmodes carbo Boh. & Men. 1♂
Podalonia communis Cresson 2♂♂
Podalonia luctuosa Smith 2♂♂
Tachysphex aethiops Cresson 1♂
Tachysphex sp. 2♀♀

BEES

74 records, 20 species

COLLETIDAE
Colletes kincaidii Ckll. 2♀♀, 3♂♂
Colletes nigrifrons Titus 3♀♀

ANDRENIDAE
Andrena cyanophila Ckll. 2♀♀
Andrena eriogoni Ckll. 16♀♀
Andrena (3 spp.) 4♀♀

HALICTIDAE
Dufourea maura Cresson 2♀♀
Halictus rubicundus Christ 1♀, 6♂♂
Lasioglossum trizonatum Cresson 1♀
Nomia sp. 1♂

MEGACHILIDAE
Anthidium tenuiflorae Ckll. 1♂
Hoplitis fulgida Cresson 2♀♀
Hoplitis producta interior Mich. 1♀
Megachile brevis Say 1♀, 3♂♂
Osmia calla Ckll. 3♀♀
Osmia indeprensa Sandh. 1♀, 1♂
Osmia tersula Ckll. 5♀♀
Osmia trevoris Ckll. 12♀♀
Stelis monticola Cresson 2♀

ANTHOPHORIDAE
Epeolus gabrielis Ckll. 1♀
Nomada sp. 1♀

Returning females descend to the nesting area from a considerable height, often landing on the ground with an audible "plop," although when followed by *Senotainia* flies they often undertake a circuitous flight close to the ground before entering their nests (Figs. 11, 13). Provisioning females were often followed by as many as four *Senotainia trilineata* Wulp. Female *Phrosinella pilosifrons* Allen were also frequently seen digging into closed nest entrances. Both species of flies were reared from cell contents, emerging in May, 1968; however, the percentage of parasitism did not appear high, in the vicinity of 20 per cent of the cells excavated. Bombyliid flies (*Exoprosopa dorcadion* O. S.) were seen ovipositing in nest entrances, and conopid flies (*Zodion fluvipes* Say) were seen following females, but I have no evidence that these species successfully parasitize *Philanthus*.

Philanthus bicinctus (Mickel). MOR-B, July 25, 1 ♀; HHS, July 23, 1 ♀.

Although this species did not nest in abundance in the areas of study, it is very plentiful at the South Gate of Yellowstone National Park, and has been studied there by Armitage (1965). This is a large, colorful species which makes very deep nests and preys primarily on bumblebees (males and workers of eight species of *Bombus*, but especially *B. bifarius* Cresson and *B. occidentalis* Greene). The male of this wasp is colored very differently than the female, and has been known as *Philanthus hirticulus* (Mickel). *Metopia argyrocephala* (Mg.) has been taken following provisioning females to their nests.

Philanthus pacificus Cresson. MOR-A, Aug. 3–26, 5 ♀♀, 6 ♂♂, ♂ on Sol; ELK, July 28–Aug. 9, 2 ♀♀, 9 ♂♂. Note nos. 2047, 2151, 2163, MOR-A; note nos. 2144, 2159, ELK: all nesting behavior.

This small species inhabits fine-grained, alluvial sand close to the riverbank or along sandy roads; at MOR there was no overlap in nesting sites with other species of the genus, but at ELK a few were nesting within the limits of the *zebratus nitens* colony. This is a late season nester and utilizes very small prey, mainly Halictidae (List 9). On no occasion did I find more than six females nesting in one area, and nest entrances were generally widely spaced. On one occasion two females were seen digging only 15 cm apart, but they attacked one another periodically. It appeared that some females made several successive nests close together, only a few centimeters apart. No more than three cells were found in any one nest, although it seems probable that more cells are occasionally constructed from one burrow (Fig. 35). Prey is often stored in the bottom of the oblique burrow, as in *pulcher* and several other species of this genus. Cells measured about 10 × 16 mm and tended to be about 4–5 cm apart; cell depth varied from 11–14 cm. The number of bees per cell varies from 8 to 15, and the egg is laid on the topmost bee in the usual manner of this genus. The mound of soil at the nest entrance is leveled thoroughly, as in *pulcher*; no accessory burrows were noted; a closure is maintained when the female is away from the nest. None of the six cells excavated appeared to be parasitized, but several *Senotainia trilineata* Wulp were seen following prey-laden females.

LIST 9

Prey records for *Philanthus pacificus* Cresson, Jackson Hole, Wyoming

WASPS

10 records, 6 species

CHRYSIDIDAE
Genus and species? 1

SPHECIDAE
Crossocerus maculiclypeus Fox 1♀
Diodontus ater Mickel 1♂
Diodontus gillettei Fox 2♀♀
Lindenius columbianus Kohl 3♀♀, 1♂
Passaloecus relativus Fox 1♀

BEES

58 records, 20 species

COLLETIDAE
Hylaeus sp. 1♀

ANDRENIDAE
Perdita fallax Ckll. 5♀♀, 1♂

HALICTIDAE
Dialictus laevissimus Smith 4♂♂
Dialictus ruidosensis Ckll. 1♂
Dialictus (10 spp.) 8♀♀, 30♂♂
Dufourea scabricornis Bohart 1♂
Evylaeus niger Viereck 1♂
Evylaeus synthyridis Ckll. 1♂
Evylaeus sp. 1♂
Halictus confusus Smith 2♂♂
Sphecodes sp. 2♀♀

Powell and Chemsak (1959) studied this species in California. They found it nesting in fine-grain sand and observed storage of the prey in short, oblique burrows, but they found no cells. In this area the prey consisted mainly of Halictidae and small Sphecidae, but they also found a braconid and an ichneumonid wasp to be used as prey.

Cerceris aequalis idahoensis Scullen. ELK, Aug. 2, 1 ♀, note no. 2132: taken from a nest of *Philanthus zebratus nitens*.

Cerceris nigrescens nigrescens Smith. MOR-B, July 8–Aug. 26, 5 ♀♀, 16 ♂♂, ♀♂ on Per, Sol; JAC, July 15, 1 ♂. Known to nest in the ground and prey on small weevils.

Eucerceris flavocincta Cresson. MOR-B, July 25–Aug. 26, 3 ♀♀, 1 ♂, ♀ on Per, ♂ on Sol; JAC, July 15, 5 ♀♀; PCR, Aug. 2, 1 ♀; HHS, Aug. 1, 1 ♂. Note no. 2137, MOR-B, Aug. 4, 1967: nesting behavior.

Female first seen on July 25, perched on a sagebrush and then plunging into a hole in a bare spot in coarse, hardpacked, stony soil only two meters from a high bank along the river. There was no mound of soil at the nest entrance. Several *Hoplisoides spilographus* also nested here. I did not see the female again, but dug out the nest August 4 and found seven cells at depth of from 7 to 10 cm (Fig. 34). The female was inside the burrow at a depth of 6 cm. The cells were well separated and the connecting burrows could not be traced. Three cells contained cocoons, two contained larvae, and one contained an egg laid longitudinally along the venter of a weevil; the contents of the seventh cell had deteriorated. Cells contained six or seven weevils each, of three species well mixed, but all of similar size and appearance. Of ten weevils identified, three were *Panscopus aequalis* (Horn), three were *Peritaxia rugicollis* Horn, and four were *Dyslobus* sp. The genus *Dyslobus* was reported as prey by Scullen (1939) in Oregon; Bohart and Powell (1956), working in California, reported a genus of weevils near *Dyslobus* to be used as prey.

Eucerceris fulvipes Cresson. MOR-B, July 28–Aug. 26, 4 ♀♀, 26 ♂♂, ♂ on Sol, Per; HHS, Aug. 11, 1 ♂; PCR, Aug. 2, 8 ♂♂; ELK, July 28–Aug. 10, 2 ♀♀, 5 ♂♂, 2 ♂♂ taken from nests of *Philanthus zebratus nitens*. Note nos. 2038, 2048, MOR-B2, Aug. 8–14, 1964: nesting behavior.

Several females were found nesting in hard, stony soil in the midst of a colony of *Philanthus crabroniformis*. In each instance the nest entrance was surrounded by a rim of soil and was left open at all times. Wasps were seen carrying weevils into these holes, holding the prey well forward, probably with their mandibles. Two burrows were excavated. One formed about a 70° angle with the surface and was traced for 10 cm, where it terminated blindly; one cell was found at a depth of 5 cm, several centimeters from the burrow. The other nest contained five cells at depths of 9–10 cm; the cells were closely grouped, and each measured about 7 × 12 mm. Each cell contained 12–18 weevils; in two cases one of the top weevils bore an egg longitudinally along the venter. Of 59 weevils taken from the four cells, all but two were of one kind, a very small species with a pale dorsal spot, *Ceutorhynchus punctiger* Gyll. The other two specimens were slightly larger, one *Brachyrhinus ovatus* L., the other *Hyperodes* sp.

In digging out one nest, a female cuckoo wasp, *Hedychrum parvum* Aaron, was found deep in the burrow (near a female *Eucerceris*). One provisioning female was seen to be followed by a miltogrammine fly, *Taxigramma heteroneura* (Mg.).

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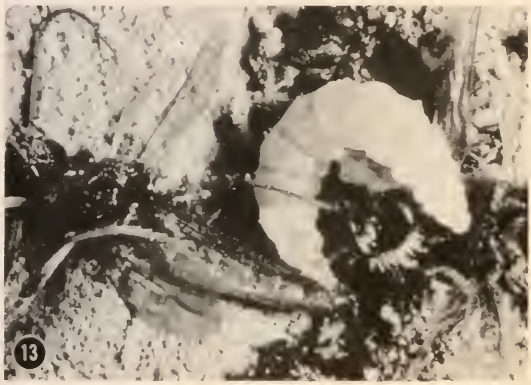
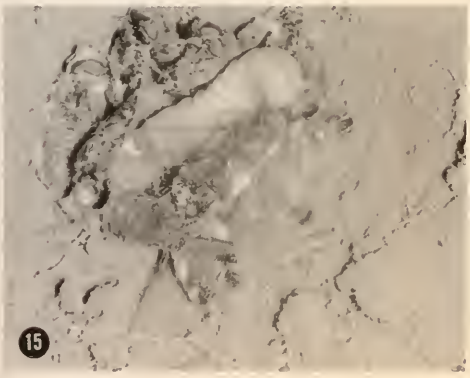
Plate I

Fig. 1. Study area MOR-A2, alluvial sand along Snake River near Jackson Hole Research Station (see Maps 1, 2). Fig. 2. Study area MOR-B3, a bare place in glacial outwash along a dirt road (see Map 1). Fig. 3. Study area ELK, alluvial sand along a dirt road 4 miles SW of the ELK P.O. (see Map 1). Fig. 4. Nest of *Pisanapsis clypeata*, closure removed but spiders in place, MOR-B3. Fig. 5. *Steniolia abliqua* feeding at the flowers of *Erigeron*, MOR-B.

Plate II

Fig. 6. *Episyron q. quinquenotatus*, female which has just suspended her spider, *Araneus patagiatus*, in the crotch of a plant, MOR-A. Fig. 7. Female of same species excavating burrow, MOR-A. Fig. 8. *Astata nubecula*, female holding her prey, an immature pentatomid, by the base of a front leg, MOR-B3. Fig. 9. *Bembix americana spinolae*, female closing nest (front legs in backstroke), MOR-A2. Fig. 10. *Senotainia trilineata* perched on a nail marking the nest entrance of *Philanthus pulcher*, MOR-B3.





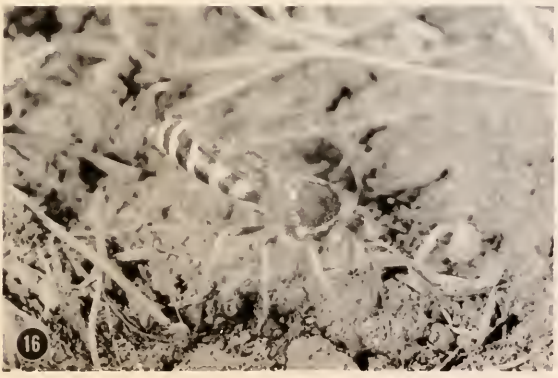


Plate III

Fig. 11. *Philanthus zebratus nitens*, female carrying prey, o male ichneuman wasp, ELK. Fig. 12. *Philanthus pulcher*, female digging at nest entrance, MOR-B3. Fig. 13. *Philanthus zebratus nitens*, larva feeding on a bee, ichneuman wasp prey on left, ELK. Fig. 14. *Phrosinella pilosifrons* digging at nest entrance of *Philanthus crabraniformis*, MOR-B3. Fig. 15. *Steniolia obliqua*, larva feeding on beefly prey in rearing tin. Fig. 16. Same species, female digging at nest entrance, MOR-A2.

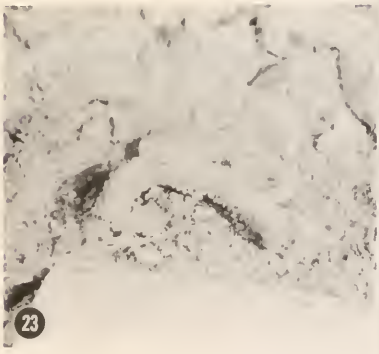


Plate IV

Fig. 17. *Podalonia communis*, female digging nest, MOR-A2. Fig. 18. *Podalonia sericea*, egg on cutworm prey. Fig. 19. *Ammaphila azteca*, female digging at nest entrance, MOR-A2. Fig. 20. Top, egg of *Ammophila macra* on hornworm prey; bottom, egg of *Ammophila azteca* on geometrid prey; both MOR-A2. Fig. 21. *Pseudomasaris vespoides*, four-celled mud nest found on top of rock at South Gate of Yellowstone. Fig. 22. *Euodynerus castigatus*, five-celled nest found under stone near Ithaca, N.Y. (this species also occurs in Jackson Hole). Fig. 23. *Stenodynerus papagorum*, mud turret at nest entrance, MOR-A2.

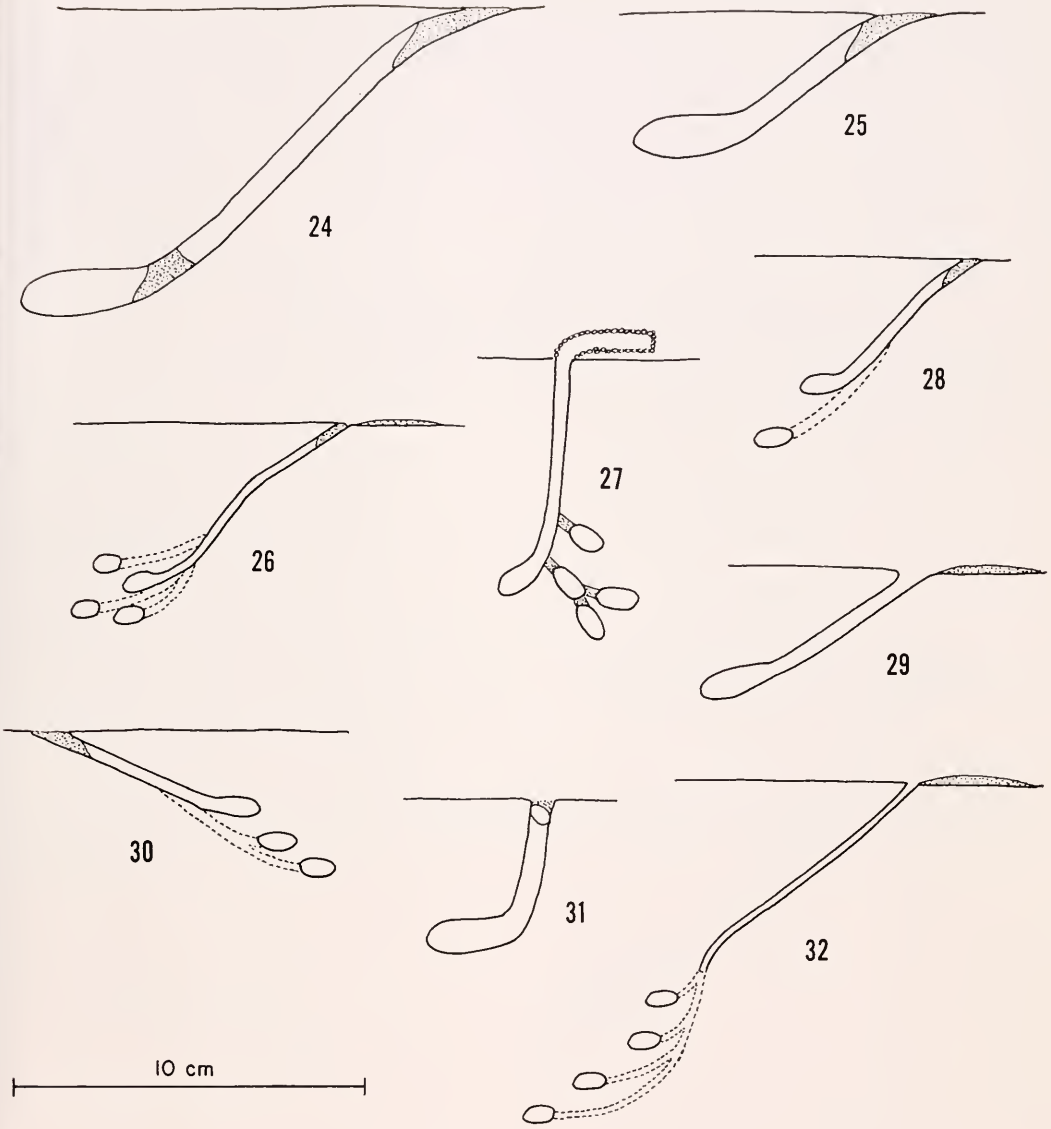


Plate V

Representative nests from study area MOR-A2, drawn to same scale (lower left). Fig. 24. *Bembix americana spinolae*, no. 2010. Fig. 25. *Steniolia obliqua*, no. 1784. Fig. 26. *Oxybelus uniglumis quadrinotatus*, no. 2104. Fig. 27. *Stenodynerus papagorum*, no. 2015. Fig. 28. *Hoplisoides spilographus*, no. 2006. Fig. 29. *Episyron q. quinquenotatus*, no. 1771. Fig. 30. *Tachysphex terminatus*, no. 2016. Fig. 31. *Ammophila azteca*, no. 2018. Fig. 32. *Diodontus argentinae*, no. 2004. Burrows which were filled and could only be approximated are indicated by dashed lines.

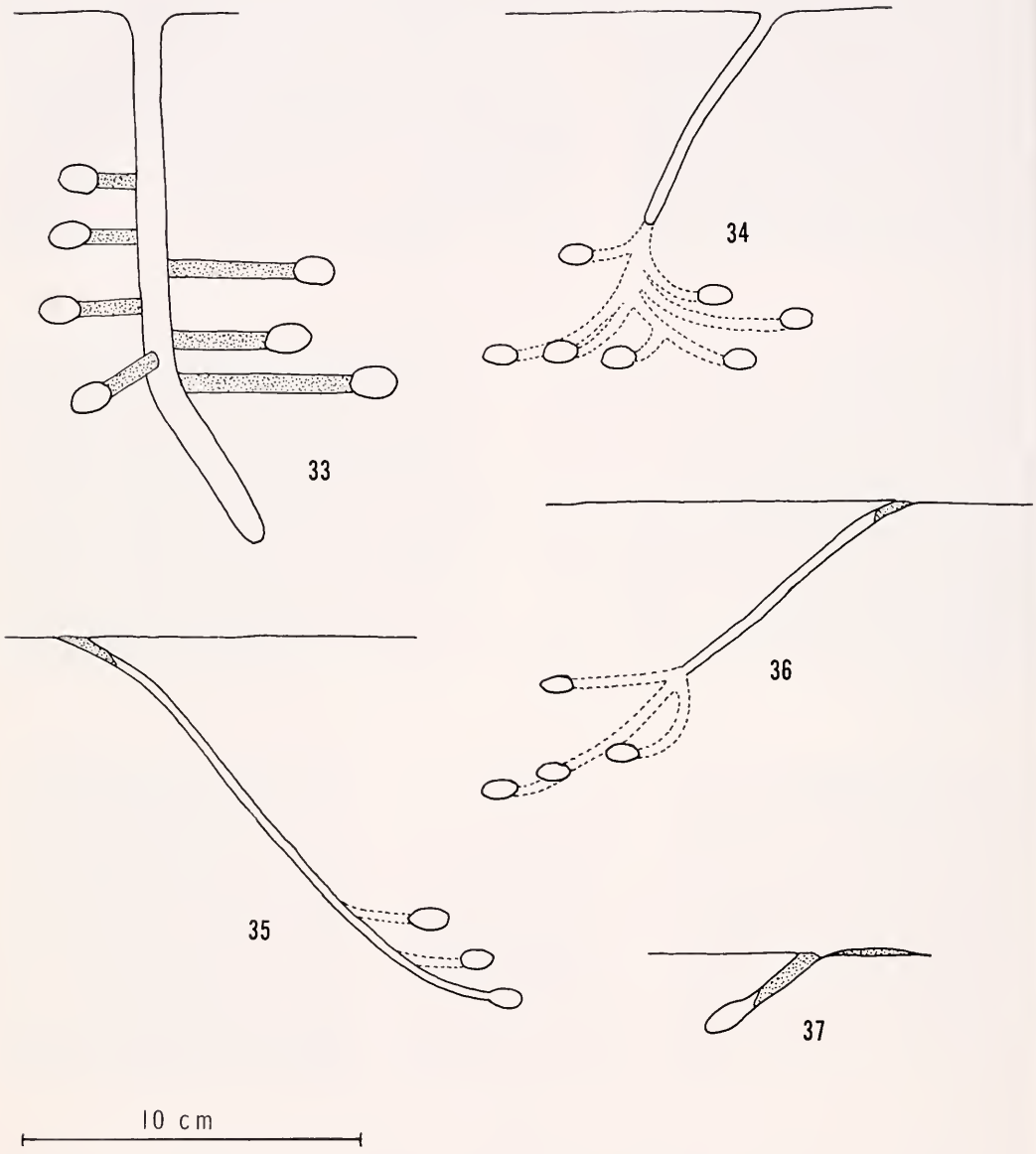


Plate VI

Representative nests of Pompilidae and Sphecidae. Fig. 33. *Cryptocheilus t. terminotum*, seven celled-nest built from walls of a cicada emergence hole, no. 2170, MOR-B3. Fig. 34. *Eucerceris flovocincta*, seven-celled nest, no. 2137, MOR-B1. Fig. 35. *Philanthus pacificus*, three-celled nest, no. 2163, MOR-A2. Fig. 36. *Philanthus pulcher*, four-celled nest, no. 2109, MOR-B3. Fig. 37. *Philanthus pulcher*, resting burrow of male, no. 2101, MOR-B3.

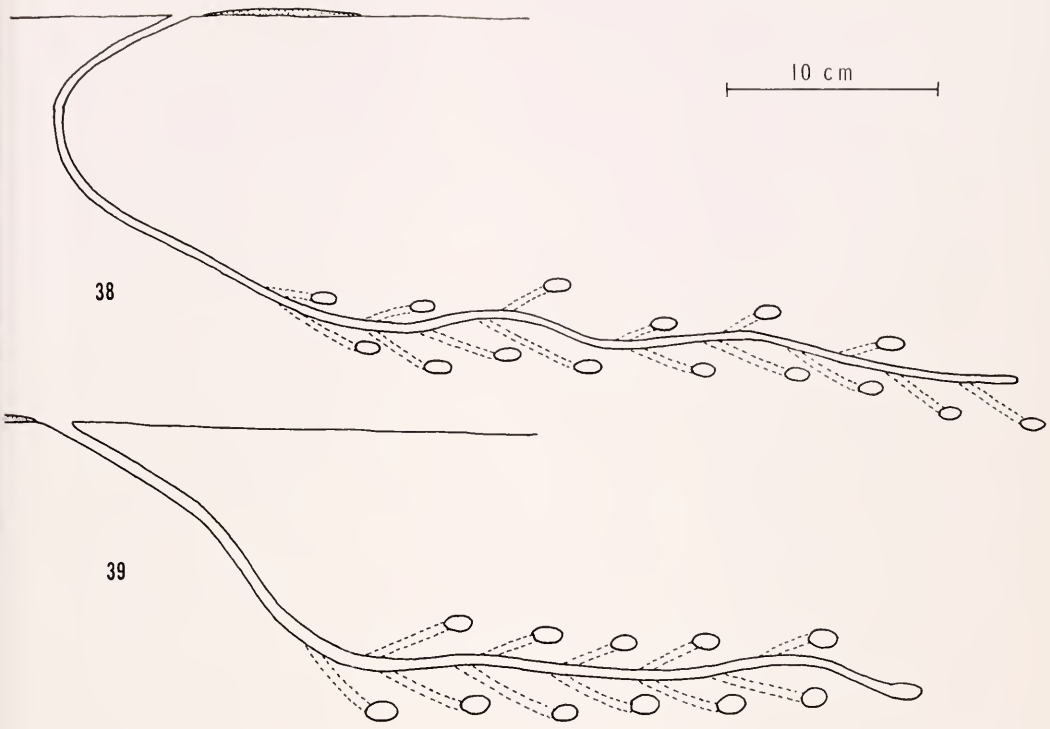


Plate VII

Fig. 38. Nest of *Philanthus crabroniformis*, no. 2173, MOR-B3. Fig. 39. Nest of *P. zebratus nitens*, no. 2155, ELK. Both somewhat diagrammatic; side-burrows to cells were packed tightly with soil and could not be traced accurately (shown as dashed lines).

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